Priming of eye movements by masked stimuli

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Contents

Summary

In a metacontrast paradigm I investigated how central symbolic and peripheral spatial primes influenced saccadic eye movements initiated by a target stimulus. Saccadic reaction times were a function of angular difference between movement directions indicated by prime and target (congruence). Saccades started earlier with high congruence than with low congruence (priming effect). In incongruent trials, gaze trajectories deviated away from the direction indicated by the prime (prime suppression). The priming effect and prime suppression increased with interstimulus interval between prime and mask. Response speed and congruence predicted the direction of gaze deviations. Gaze deviations towards or away from the prime seemed to reflect the relative timing between the onset of prime-suppression with respect to movement initiation. The effect of primes on saccadic reaction time and metrics were simulated in a neural network model based on the assumption that decision processes and response preparation both rely on population coding as their principle of neural representation. The model accounts for the reaction time data as well as for the observed gaze deviations.

"... it will be safe to lay down the general law that no mental modification ever occurs which is not accompanied or followed by a bodily change."

"And a very small amount of reflection on facts shows that one part of the body, namely, the brain, is the part whose experiences are directly concerned."

William James, 1890

Chapter 1

Introduction

Previous experiences affect our performance in multiple ways. We can usually recognize objects better and faster if we have seen them before, even if we have no conscious memory of having seen them (Schacter et al., 1990, 1991; Squire, 1992). If in a series of events, a first event, the prime, correctly predicts critical attributes of the second event, the target, response times are faster compared to an incorrect prediction (Posner, 1978, 1980). This phenomenon is called *priming*. Priming operates on any perceptual stimulus attribute as identity, shape, color, orientation, location, and movement, as well as on attributes of the response. And it is effective even if the prime does not exist physically in the external world, but only in imagination (Kosslyn, 1988). Congruent primes are assumed to facilitate processing of the target whereas incongruent primes are assumed to create interference. It is commonly believed that priming is due to a tendency of neuronal populations to be more easily activated if they have been activated previously. As stated by Hebb (1949) "Each assembly action may be aroused by the preceding assembly, by a sensory event, or –normally– by both."

The experimental studies and simulations I will present in the following chapters are aimed at the question of how primes, whose visibility is reduced by visual masking, influence responses to subsequent targets. Temporal spacing between prime and target and their degree of congruence will be of special interest in order to probe the central assumption that time and similarity determine the coactivation of neuronal assemblies, which represent primes and targets.

Outline

Chapter two provides a description of fundamental findings about the dissociation of perception of primes and their effects on subsequent actions. It further introduces an accumulator model which accounts for priming effects in two-alternative choice reactions. An extension of the paradigm to priming with different degrees of congruence is proposed, using eye movements as the required response. Chapter three presents four experimental studies on the effect of central symbolic and peripheral spatial primes on eye movements. The findings are related to previous experiments using manual reactions and to the predictions of the accumulator model. Chapter four presents an extended model and simulations thereof, to account for the observed reaction times and trajectories reported in the experimental section.

Chapter 2

Dissociating perception and priming

1.1 Metacontrast masking

When presenting a visual test stimulus, for example a small white disc on a dark background, it can clearly be perceived, even if presentation time is shorter than 10 ms. Such a stimulus can be rendered less visible or even invisible by presenting a second stimulus in short succession. This phenomenon is called backward masking because the second stimulus, the mask, seems to operate backward in time, when it destroys the percept of the first stimulus. A special kind of backward masking is *metacontrast masking* (Stigler, 1910; Werner, 1935; Fehrer and Raab, 1962) in which test stimulus and mask neither overlap in time nor in space. In the classical metacontrast procedure the test stimulus is a disc and the mask a surrounding annulus (figure 1). Both stimuli are presented centrally with varying stimulus onset asynchrony (SOA). The subjects' task is to indicate the subjective brightness of the test stimulus in order to obtain a masking function.

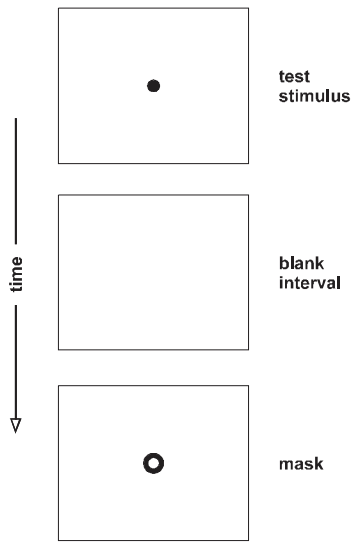


Figure 1: Disc-annulus procedure of metacontrast (Werner, 1935). The duration of the blank interval is varied, which leads to different SOAs of test stimulus and mask. Note that brightness is reversed here, stimuli are presented light on dark.

Strength of masking depends on three factors: SOA, the relation of light energy between prime and mask, and their spatial separation. If the energy of the mask is greater than that of the test stimulus, masking decreases monotonically with SOA until reaching an asymptote (type-A masking). If the energy of the test stimulus exceeds that of the mask, the masking function is nonmonotonic (type B-masking), with weak masking at short and long SOAs and strong masking at SOAs between 40 and 80 ms (Breitmeyer, 1984). Masking becomes weaker with spatial separation of test stimulus and mask (Growney et al., 1977).

When the task is changed to pressing a button as soon as the test stimulus appears, one would expect that a stimulus, which is only weakly masked, produces shorter reaction times than a stimulus that is barely perceived. Surprisingly, reactions triggered by the test stimulus are not delayed when it is masked. Reaction times are unaffected if not speeded up over the entire SOA-range in the masked condition compared to presenting the test stimulus alone (see Breitmeyer (1984) for an overview).

1.2 Priming without awareness

Is it possible that metacontrast affects the conscious perception of the test stimulus, but leaves intact the stimulus' ability to trigger a motor response? Can stimuli, which remain unaware, control behavior? This is the central issue of the theory of direct parameter specification (Neumann, 1989, 1990). The theory postulates that processing of a stimulus can specify parameters without mediation by a conscious representation of that stimulus. Neumann and Klotz (1994) tested this claim in a series of experiments using an extended metacontrast procedure. They changed the task from a simple reaction to the appearance of the test stimulus into a masked priming task that required choice reactions to attributes of the mask. In contrast to the terminology used above, the stimulus, which appears first, is termed *prime* from hereon. The second stimulus, to which the subject reacts and which masks the prime, will be called *target*. A fundamental question of their experiments was whether choice reactions to the target could be primed without subjects being aware of the prime.

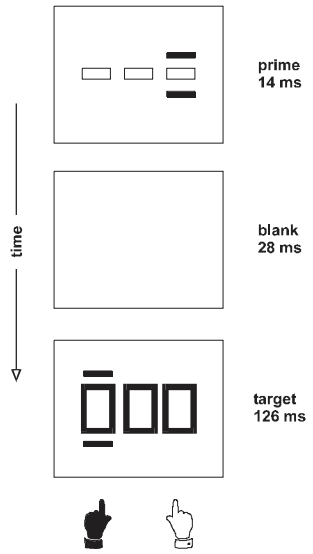


Figure 2: Temporal sequence of a masked priming trial in Neumann and Klotz (1994). The prime, containing flankers on the left or the right side in half of the trials, is briefly presented. After a fixed blank interval, the target is shown, which masks the prime. Flankers of the target indicate which response key to press.

Primes were presented for 14 ms, and masked after a fixed SOA of 42 ms. The target consisted of three horizontally arranged boxes. The left or the right box contained markers above and below indicating which response key to press. The prime consisted of three flat boxes. The left or the right box of the prime contained markers in half of the trials. Prime size was chosen so that the prime fitted into the boxes of the target (figure 2). The critical attribute of primes and targets was the location of their flankers. A prime was called congruent when its flankers were presented on the same side of fixation as the flankers of the target, and incongruent when prime and target flankers were on opposite sides, and neutral if prime markers did not have flankers.

Two tasks were administered in separate parts of the experiment: 1) priming and 2) detection. In the priming task subjects were instructed to press the button on the side on which the marked box had appeared. Detection was a replication of the priming task, only that subjects now had to index their confidence on a rating scale that the prime contained a marked box.

The results were striking. Although subjects were unable to detect the prime ($d' = 0$), primes had a strong influence on reaction time and errors. When primes and targets where congruent, reaction times were 50 ms shorter than in trials in which primes and targets were incongruent, and 14 ms faster than with neutral primes. Error rates were highest under incongruent and lowest under congruent conditions. In a further experiment Neumann and Klotz introduced compatible and incompatible stimulus-response-mappings (SR-mappings). In incompatible blocks, subjects had to press left when the imperative stimulus appeared at the right and vice versa. Even under these conditions the priming effect remained stable.

The results provided clear evidence for priming without awareness. Masked stimuli, which did not enter awareness, nevertheless did influence choice reactions to the target. Further, when SR-mappings (compatible vs. incompatible) were changed unpredictably from trial to trial, the same priming effects were observed, again without subjects being aware of the primes. Although processing of the prime did not result in its conscious perception, its processing was sensitive to the compatibility-instruction. This implies that the theory of direct parameter specification not only applies to hard-wired or overlearned SR-mappings, but also to situations in which stimulus and response are dynamically linked. Direct parameter specification finally broke down when the information about SR-mappings was given as short as 250 ms before the trial, suggesting that action planning was not finished when the prime was presented.

1.3 Different systems for perception and action

Recent research with neurological patients (Goodale et al., 1991; Köhler and Moscovitch, 1997; Weiskrantz, 1997) and healthy subjects (He et al., 1996; MacLeod, 1998; Merikle and Danemann, 1999) has presented evidence of behavioral effects of stimuli, which remain outside awareness. This does not necessarily mean that perception and action are performed by separate systems in the brain. An alternative explanation and common criticism concerning this type of dissociation is that there are conditions under which the authors were able to measure behavioral effects while failing to show perceptual effects due to methodological flaws or due to the impossibility to prove the null-hypothesis. To advance the position of different systems for perception and action, one needs to show more than the existence of action without perception, but that perception and action obey different laws.

Vorberg et al. (in prep.) employed this strategy. They investigated whether perception and action follow the same time course. The temporal dynamics of masking are well understood (Breitmeyer, 1984; Francis, 1997), but what are the temporal dynamics for priming with and without awareness? Vorberg et al. used left and right arrow shaped stimuli as primes and targets in a metacontrast procedure with choice reactions. The prime arrow was briefly presented above or below fixation, and followed by the target arrow after a variable SOA at the same location (fig. 3A). The time course of masking was measured by asking the subjects to respond to the orientation of the primes. The time course of priming was studied in a speeded choice reaction task to the orientation of the target. Prime and target were called congruent if they had the same orientation, and incongruent otherwise. Two experiments were conducted: Experiment 1 investigated priming without awareness (subliminal priming) and experiment 2 addressed priming with awareness (supraliminal priming).

Experiment 1 consisted of three priming and two masking parts, here simply referred to as priming and masking (see Vorberg et al. for further details). The speed of manual choice responses depended on prime-target congruence (fig. 3B): Reaction times with congruent primes were shorter than with incongruent primes, replicating previous results (e.g. Neumann and Klotz, 1994). In addition, the experiment revealed that priming increased with temporal separation between prime and target. The priming function ($RT_{incongruent} - RT_{congruent}$) increased almost linearly with SOA (fig. 4A, lower panels). However, the masking function showed that subjects performed at chance level over the entire SOA-range when responding to the orientation of the prime. Experiment 1 presented clear evidence for subliminal priming over a large range of SOAs. But for reasons mentioned above, the finding of priming without awareness may not be sufficient to postulate that perception and action obey different laws.

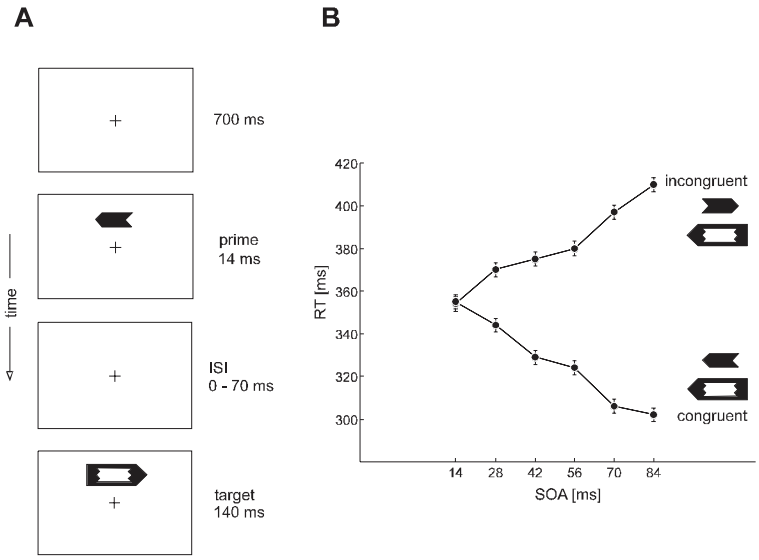


Figure 3: **A**, Temporal sequence of a typical priming trial in the Vorberg et al. study. Left and right oriented arrows served as prime and target stimuli. Primes fitted exactly into the center cut out of targets. Orientation of prime and target varied unpredictably from trial to trial. Congruent and incongruent trials occurred equally often. **B**, Effects of congruent and incongruent primes on choice RT as a function of SOA in the first session of Experiment 1. Error bars indicate ± s.d. around means. **C**, The priming effect increased almost linearly with SOA (after Vorberg et al.).

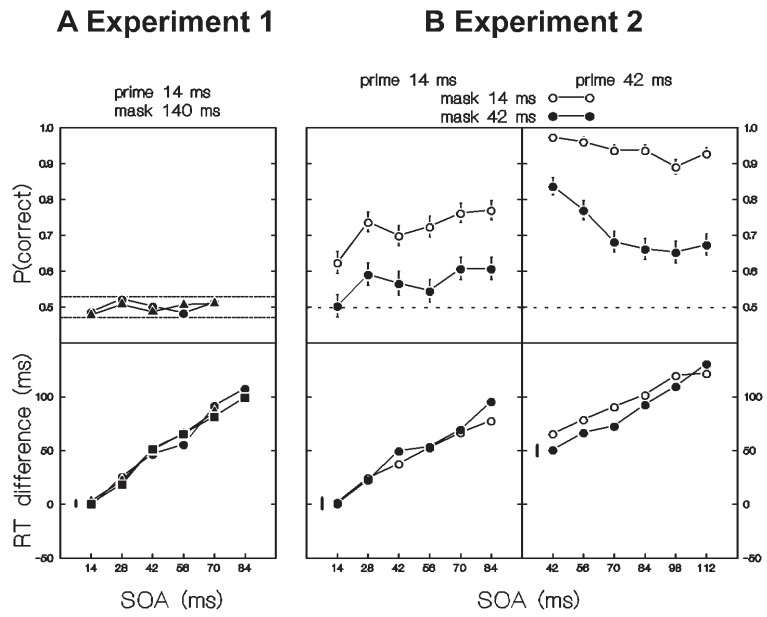


Figure 4: Masking and priming functions obtained in experiments 1 and 2 of Vorberg et al. (in prep.). **A**, Experiment 1. Top row: Masking functions (parts 3 and 4). Subjects performed at chance level (dotted lines indicate the confidence interval for p = .5). Bottom row: Priming function (for parts 1, 2, and 5). **B**, Experiment 2. Short primes gave rise to type A masking, long primes produced type B masking (upper row). Despite of qualitative changes in masking, priming functions remained invariant.

Therefore Vorberg et al. tested for dissociations of action and perception with supraliminal priming. In Experiment 2 target duration was generally shorter than in experiment 1 (140 ms) to increase prime visibility. Short (14 ms) and long (42 ms) presentation times were factorially varied for primes and targets. Subjects recognized primes above chance (figure 4B, upper row). Target duration had an additive effect. Long targets produced stronger masking than short targets, but did not change the shape of the masking function. Varying prime duration produced qualitative changes in the masking function. Masking decreased with SOA when short primes were used (type A masking). Long primes resulted in type-B masking (U-shaped visibility of the prime).

The main finding of the Vorberg et al. study is that priming effects were not at all affected by the variations of prime visibility. Primes followed by long targets produced the same reaction time effects as primes, which were followed by short targets, although prime visibility was changed by this experimental variation. Finally, using long primes, perception of the prime was U-shaped (type B masking) while their effect on choice reactions to the target constantly increased. This finding is the most convincing psychophysical evidence for a dissociation of perception and action reported so far: *Perception and action follow different temporal dynamics*.

1.3.1 An accumulator model of priming

Vorberg et al showed that the priming effect in Experiment 2 followed the function $RT_{incongruent} - RT_{congruent} = SOA + b$, where the intercept b was equal to zero except for the long primes. They proposed an accumulator model which collects neural evidence for primes and targets in separate accumulators for left and right responses (figure 5). Accumulators were subject to saturation, due to random decay of spike effects. Response tendency at time t was defined as the difference D(t) between the current accumulator states. A response was initiated if D crossed threshold c.

Accounting for the observed unit slope in priming proved to depend critically on the nature of the accumulation process. The problem is illustrated in figure 6, in which an accumulation process without saturation is assumed. The number of spikes, which indicate evidence for a stimulus pointing left or right, is simply counted. The presence of primes produces spikes that feed accumulators for SOA ms. If primes and targets are congruent, primes drive the difference D towards the critical threshold for the correct response, and the process continues indistinguishable after presentation of the target. Incongruent primes drive D away from the appropriate threshold for a duration of SOA ms. After presentation of the target, driving the response tendency back to balance (D = 0) takes another SOA ms, before D shifts towards the appropriate critical threshold c. Consequently, accumulation without saturation results in a priming effect:

$RT_{incongruent} - RT_{congruent} = 2SOA$, which is at odds with the data.

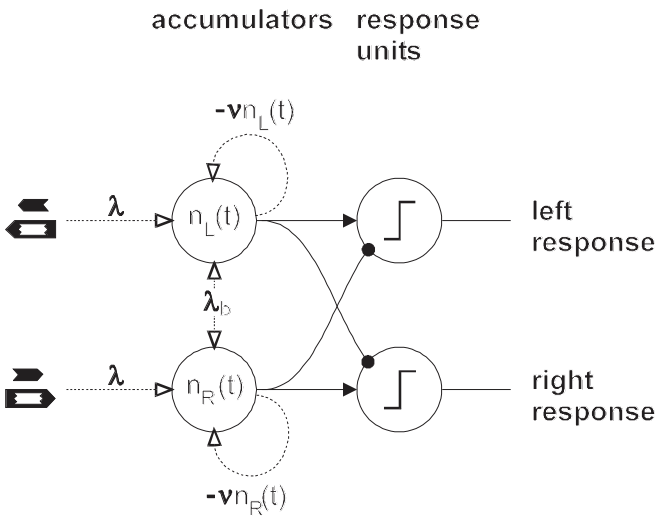


Figure 5: Accumulator model of priming. Input spike trains are modeled as inhomogeneous Poisson processes by which spikes with rate λ increment state *n* of two accumulator units for left and right responses, respectively. Primes and targets are processed identically. Accumulators show saturation due to random decay of spike effects (rate *ν*). Responses are initiated when the difference *D(t)* between the accumulator states crosses threshold (from Vorberg et al., in prep.).

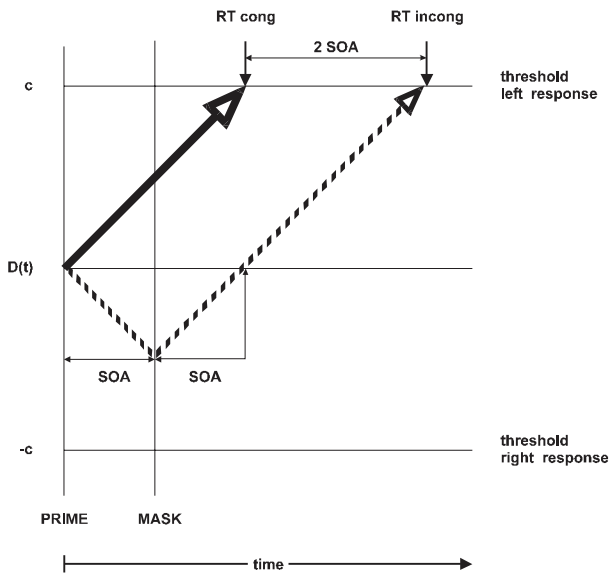


Figure 6: Effect of accumulation without saturation. Example for a target pointing to the left, which is preceded by a congruent (black) or an incongruent prime (dotted line). Congruent primes drive the difference between accumulators (D) towards threshold (c) of the correct response and incongruent away from it. When the target is presented after SOA ms, D simply proceeds toward threshold, and a response is initiated once threshold is crossed (RT_{cong}). With incongruent primes, responses are delayed, due to the fact that SOA ms were spent preparing the wrong response, and that it takes another SOA ms, before D reaches baseline. From thereon, D proceeds towards threshold, and initiates the appropriate response after crossing threshold (RT_{incong}). Thus, incongruent primes delay responses by the duration of 2SOA compared to congruent primes.

Vorberg et al. showed through mathematical analysis of the means of the accumulators' states and by way of Monte Carlo simulations of the stochastic model that the following conditions must be met to explain the observed priming effects with accumulator models:

1) Primes and targets are processed identically

2) Accumulators obey saturation.

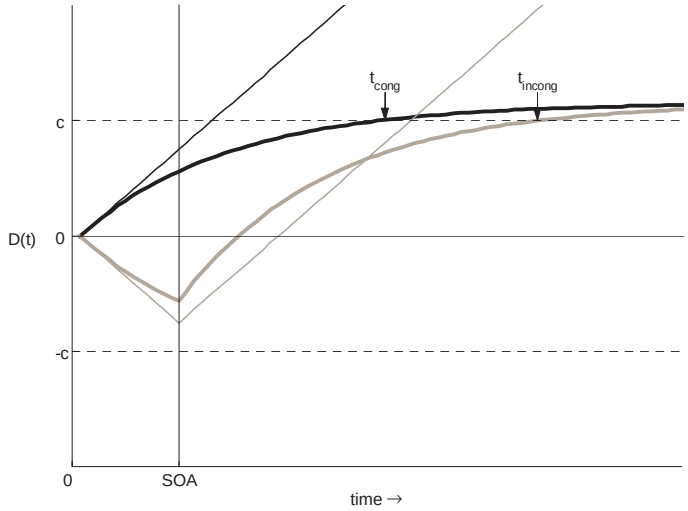
They proved that in such a model, slope of priming function is insensitive to processing rate and threshold, but depends critically on degree of saturation. Slope of priming functions is bound between 1 and 2, with higher saturation leading to smaller slopes. Instead of repeating the mathematical analysis presented by Vorberg et al., a graphical description, based on a simple physical model, is offered to illustrate the role of saturation in priming.

1.3.2 A rubber band illustration of saturation effects

Suppose, D(t) being the distance of a motorized toy-car from its starting position at a particular time t, with D(0) = 0. The car can move left- or rightwards. Connecting the car with a rubber band to the starting point induces saturation. While moving towards the finish line (c) the movement of the car decelerates, because the pulling force of the rubber band increases with distance (|D|). Analogous to priming experiments, the car has the correct direction right away (congruent), or it moves in the opposite direction (incongruent prime) for a specified time (SOA), and is then turned around. We want to know, how long it takes the car to travel the distance from start to the finish line (when it passes threshold c) under congruent an incongruent conditions. Compared to a situation without saturation, in which the car moves without rubber band, the following will be observed (see figure 7):

In the congruent condition, threshold is reached later with than without saturation, because the pulling force of the rubber band hinders the car. In the incongruent condition, once the car is turned around, it reaches baseline **earlier** with than without saturation, because a) it has traveled a shorter distance so far, thus the way back to baseline is shorter, and b) it proceeds **faster** towards baseline, because it is pulled back by the rubber band. Consequently, the delay of $D(t)_{incongruent}$ with respect to $D(t)_{congruent}$ becomes shorter than under conditions without saturation, leading to a difference of elapsed time ($t_{incongruent} - t_{congruent}$) smaller than 2SOA when crossing threshold.

A



B

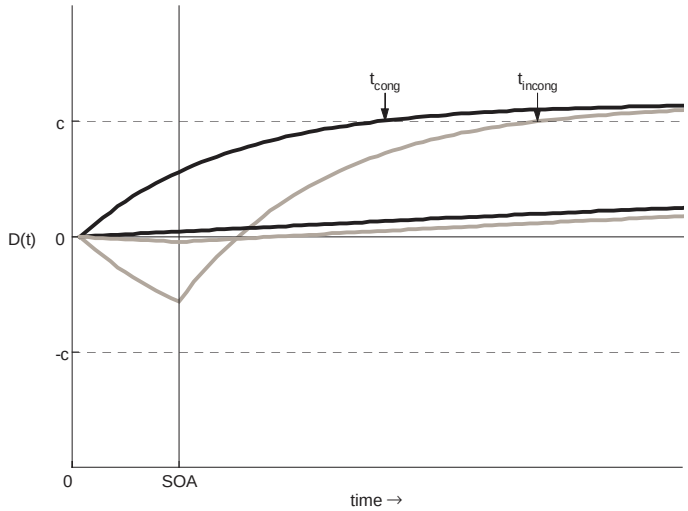


Figure 7: The effect of saturation on response delay. Distance over time, D(t), of a moving object from initial position is shown. The object either moves continuously from start to finish line (congruent condition, black), or in the opposite direction (incongruent condition, gray) until it is turned around, when a turning signal is given at a specific time (SOA). Time until crossing finish line (D(t) > c) is indicated for congruent (t_{cong}) and incongruent (t_{incong}) conditions. **A**, Slope of $t_{incong} - t_{cong}$ equals 2SOA with no saturation (linear functions). Slope is less than 2SOA with saturation (negatively accelerated functions). **B**, Shape of D(t) changes from a negatively accelerated to a linear function with saturation approaching maximum, and t_{incong}-t_{cong} converges towards SOA. See text for further explanation.

The pulling of the rubber band applies to all required target distances, and it would affect trucks, too. This means that the slope of the priming effect will always be smaller with than without saturation, given the other parameters remain constant, and that this is true for any threshold and processing rate. What has not been shown in the example, but by Vorberg et al., is that the priming effect actually is *unaffected* by threshold and rate. However, their critical finding, that the slope of the priming effect depends on the level of saturation, can be easily understood now. If the rubber band is very long (and has no weight) it does not pull, and the time course of the car is along the straight lines in figure 7 (panel A), resulting in a slope of 2 for the priming effect (see figure 6). With shorter rubber bands (increasing saturation) stronger pulling forces are applied while moving away and towards baseline, which leads to smaller priming effects.

Vorberg's finding that the priming effect becomes linear with a slope converging towards 1 (unit slope) is illustrated in panel B of figure 7. With strong saturation, D(t) starts flat, being already close to linearity. Secondly, incongruent primes drive D only minimally away from threshold. When the target is presented with any SOA, D is driven back to baseline (almost) instantaneously. Taken together, this results in two linear functions with the same slope and intercept, but different start times (SOA). Consequently, for each threshold and SOA, the time difference when threshold is crossed in the congruent and in the incongruent conditions equals SOA.

1.3.3 The relation between threshold, errors and priming

The accumulator model allows detailed predictions about errors. An error occurs in the model if the threshold –c for the incorrect response is crossed. The model predicts, that the majority of errors should occur in incongruent trials, and that the likeliness of such an event increases with SOA, as incongruent primes bias response tendency towards the incorrect response. A critical test for the model is that it further predicts a dissociation between error- and priming function. Lowering the threshold should increase error rate, but leave priming functions unchanged. Vorberg et al. tested this prediction by comparing priming functions of subjects with high vs. low error rates, assuming they had different response criteria. Data and predictions are shown in figure 8. The predictions of the model were confirmed by the data: 1) error rates increased with SOA, 2) priming functions were similar for subjects who differed in error rate. Finally, the accumulator model predicts faster responses for incongruent error trials compared to correct responses under congruent conditions, because these errors are most likely due to the processing of primes, that is before the imperative stimulus is presented. This prediction was confirmed, too. Errors after incongruent priming led to reaction times that were 37 ms faster than correct responses after congruent primes.

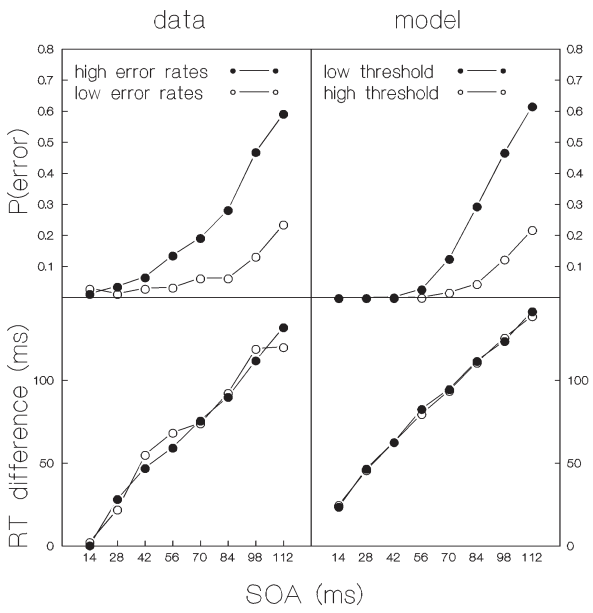


Figure 8: **Right column**, The accumulator model produces increased error rates when threshold is lowered (upper panel). In contrast, priming functions are insensitive to threshold changes (lower panel). **Left column**, Confirmation of the predicted dissociation of error rate and priming function. Comparing subjects with high and low error rates (upper panel) did not reveal any differences in the priming function (lower panel).

1.4 Issues in priming, similarity, and response preparation

The experiments of Neumann and Klotz (1994) have provided strong evidence for priming without awareness. The results support the claim of Neumann's theory of direct parameter specification that a stimulus may achieve behavioral control without being consciously mediated (Neumann, 1989, 1990). Compelling psychophysical data for a dissociation of perception and action have been presented by Vorberg et al. (in prep.), who report subliminal priming and most importantly invariant priming in the face of different perceptual effects.

Accounts for the dynamic characteristics of perceptual effects in masking are based upon a profound psychophysical basis (Breitmeyer, 1984) and seem well understood by recent work in neural modeling (Francis, 1997). A similar dynamic characterization of the action process was not formulated until the presentation of the accumulator model by Vorberg et al. The work presented in the following chapters focuses on the scope of the accumulator model and on the further characterization of priming effects:

- Does the accumulator model apply to manual reactions only, or does it also apply to eye movements? A critical test for the model is that it predicts a linear increase for the priming effect $RT_{incongruent} - RT_{congruent}$ with a slope bound between 1 and 2.

Eye movements are chosen because they can be carried out in different directions, which allows to investigate priming in more detail:

- Can masked stimuli prime eye movements in situations with more than two response alternatives?
- Does degree of congruence affect degree of priming?

Eye movements provide information on saccadic reaction time as well as on continuous kinetic measures of gaze velocity and position. This may allow gaining deeper insight into the nature of priming:

- Do primes affect only the decision when to start the saccade or do they directly affect response preparation? Interference effects should occur if masked primes induce response preparation. These interference effects could be manifest in altered velocity profiles, saccade amplitudes or in directional deviations.

These questions will be dealt with in two separate parts. Chapter three contains experimental studies of priming in eye movements. In chapter four, the experimental observations will be incorporated into a neural network model.

Chapter 3

Experiments

In this chapter, four experiments are reported which investigate the influence of masked primes on reactions to subsequent target stimuli. The purpose of all four studies is to find out whether eye movements can be primed by masked stimuli and whether the accumulator model of priming can be applied to experimental settings with more than two response alternatives and parametrically varied congruence. A second objective is to identify indicators of priming in the kinetic properties of the movements, which is relevant for the question whether primes can gain direct access to motor programming or whether they only influence decision latencies.

The experiments are based on a variation of the paradigm developed by Vorberg et al. In order to separate spatial- from shape-priming, centrally presented symbolic stimuli serve as primes and masking targets in experiments 1 and 2, whereas experiments 3 and 4 use peripheral spatial cues instead of central symbolic primes.

2.1 Experiment 1: The influence of masked primes on eye movements

Instead of two antagonistic manual responses, which were used by Neumann and Klotz (1994) and by Vorberg et al. (in prep.), saccadic eye movements with equal amplitude but different directions were required. Arrow shaped central stimuli served as primes and targets. Congruence was varied parametrically according to the angle between the different directions to which primes and targets pointed.

2.1.1 Materials and methods

Subjects. Eight subjects (6 females, two males, mean age 26.6 years ranging from 21 to 44 years) with normal or corrected to normal vision participated in 8 1-hr sessions within two weeks. Four subjects received course credits, the others were paid 10.- DM per hour. Except for the author and his research assistant, subjects were naive to the purpose of the experiment.

Stimuli. Stimuli (fig. 9) were presented centrally black on white on a 20" SONY VGA color monitor with a refresh rate of 60 Hz. The subjects viewed the stimuli from 90 cm, with their head rested on a chin rest. Primes and targets possessed an orientation ϕ by pointing to one of eight markers arranged around the center of the screen at a distance of 5°, each 0.5° in size. Targets subtended 1.3° in width and 1° in height. A prime had half the size of a target and fitted exactly into a target's central cut-out (figure 9). Neutral primes did not contain any directional information, they were employed in order to get an estimate for the baseline of priming.

Congruence between primes and targets was defined as the absolute angular difference between the orientation of target and prime, respectively (congruence = $|\phi_{target} - \phi_{prime}|$). If, for example, a target pointing upwards ($\phi_{target} = 90°$) was preceded by a prime pointing to the left ($\phi_{prime} = 180°$) the resulting congruence was 90°. Five levels of congruence (0, 45, 90, 135, and 180°) and an additional neutral condition were realized, with the latter containing a neutral prime.

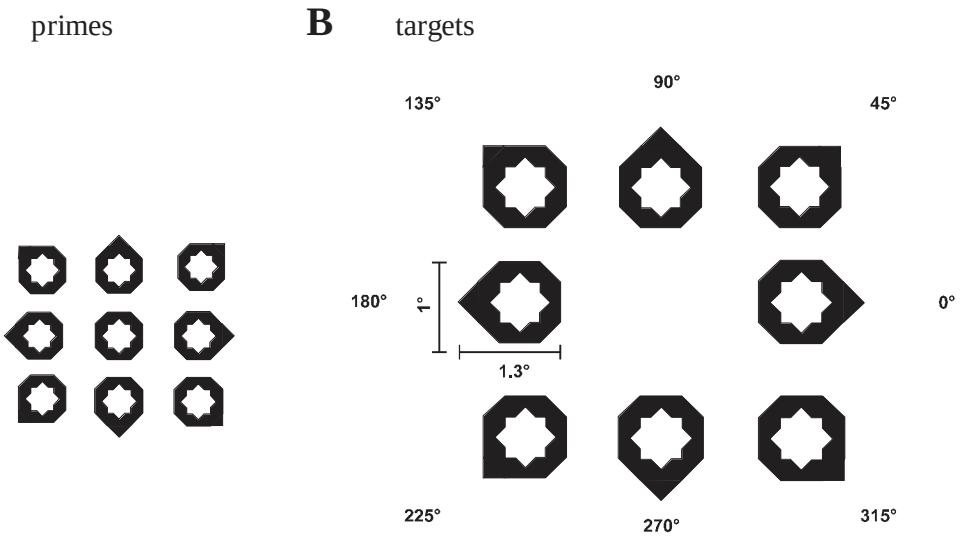


Figure 9: Oriented primes (**A**) and targets (**B**) pointed to one of eight peripheral markers indicated by the direction of the arrow head, except for neutral primes (panel A, center), which did not contain any directional information. Primes fitted exactly into a target's central cut-out.

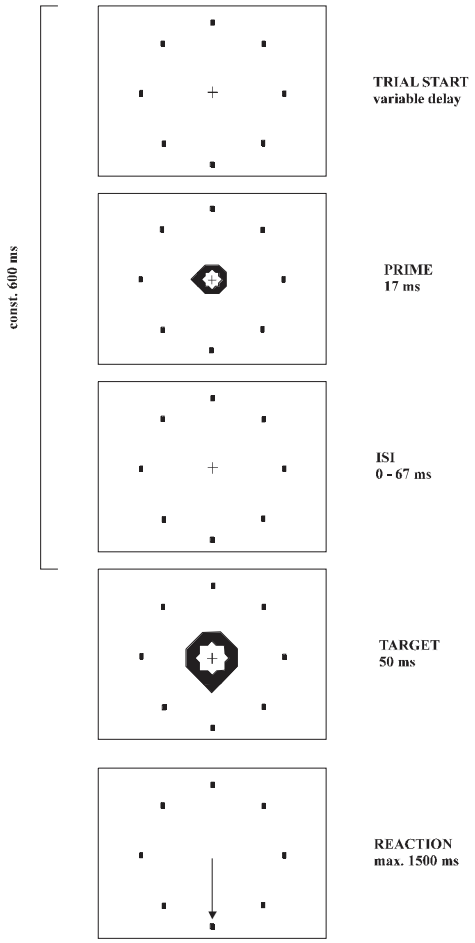


Figure 10: Subjects started a trial with a key press. After a delay a prime pointing to one of eight target positions appeared for 17ms. After a variable SOA (17 to 84 ms) a target was presented for 50ms. The subjects' task was to direct their gaze to the target position to which the target pointed. The angle between prime and target direction to varied unpredictably between 0° and 180°.

Task. The task was to perform a saccade to a peripheral mark within a speeded eight alternatives forced choice reaction. A trial began with the presentation of the fixation cross and eight surrounding position marks (figure 10). Subjects started the following sequence by a key press. After a variable delay the prime appeared for 17 ms at the center of the screen. After an unpredictable SOA between 17 and 84 ms (inter stimulus interval, ISI, between 0 and 67 ms) a central target was shown for 50 ms. In each trial, the onset of the target was kept constant at 600 ms from trial start. Subjects responded by directing their gaze as fast as possible to the marker to which the target pointed. 500 ms after fixating a target subjects were allowed to start the next trial.

Design. SOA (17, 33, 50, 67, and 84 ms) and congruence (neutral, 0, 45, 90, 135, and 180°) were varied orthogonally in a repeated measures design. Dependent variables were saccadic reaction time, amplitude, velocity, landing position and saccade contingent gaze position (see section eye movement recording below). Each subject completed eight sessions with 16 replications of each SOA - congruence combination leading to 640 trials for each congruence level and 3840 trials per subject.

Procedure. Each session began with written instructions describing the task. Possible target orientations were explained graphically. Subjects were not informed about the occurrence of primes. Subjects were told to direct their gaze in the direction of the 'large' stimulus appearing on the screen as fast as possible. Each session consisted of 480 trials with a ten-minute break midway.

Eye movement recording. Eye movements were measured with a video-based SMI Eye Link system with a temporal resolution of 250 Hz and a spatial resolution of 0.2°. The system tracks the position of the pupils of both eyes and of four infrared markers placed at the corners of the stimulus display to compensate for small head movements. The correspondence between pupil position in the eye-camera image and gaze position on the stimulus display is calculated by interpolating the positions of the actual eye camera image from nine reference positions which were recorded in a calibration procedure at the beginning of each experimental session. For calibration subjects fixated a sequence of nine calibration targets (size 0.5°) which were presented in unpredictable order on a 3*3 grid (width 24°, height 18°). Drift correction was performed at the beginning of each trial when subjects simultaneously fixated the central fixation cross and pressed a key. The actual fixation position served as the reference for the center of the screen throughout the remainder of a trial. Gaze position was available online. If during a trial a saccade end position fell within a radius of 1° of a saccade target marker, the corresponding target was counted as the subject's response and the trial was terminated. Whenever during a trial subjects fixated a target position not indicated by the target or when an eye blink occurred, the trial was terminated with a warning tone.

Data processing. The onset of a saccade was determined as the first sample in a series of at least 3 samples (12 ms) at which gaze velocity exceeded 30°/s. The end of a saccade was the sample at which gaze velocity dropped below 30°/s. Onset, amplitude, velocity, landing position, and saccade contingent gaze position (80 ms before to 80 ms after saccade onset) of the first saccade after presentation of the target (the primary saccade) were included in the offline data analysis. Saccadic reaction time was determined as the onset of the primary saccade with respect to the presentation of the target.

Error handling. Only those trials were included in the eye movement analysis in which the correct target position was fixated, the others counted as fixation errors. Further reasons for excluding trials were, if: A) saccadic reaction time was below 80 ms (anticipations), B) an eye blink occurred throughout the trial (blinks), or C) when there were low velocity eye drifts (5° < velocity < 30°).

2.1.2 Results

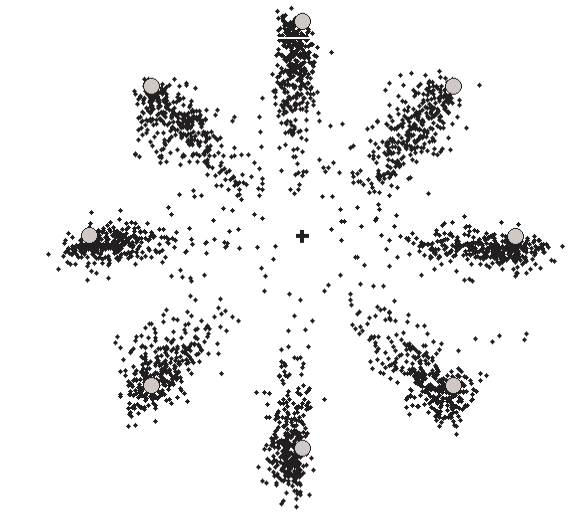


Figure 11: Saccade landing positions for each target position, congruence, SOA, and subject.

Mean landing positions of the primary saccades for each subject under each combination of conditions are shown in figure 11. The figure illustrates that hypermetric and hypometric saccades occurred, and that saccades landing positions deviated from the required direction. The following saccade parameters and their dependence of congruence and SOA will be analyzed below: saccadic reaction time to test the predictions of the accumulator model, and kinematic parameters as 1) gain, i.e. saccade amplitude divided by target eccentricity, 2) velocity, and 3) angular deviation from target direction to gain further insight in saccade dynamics and the underlying mechanisms of saccade generation.

Errors. 3840 trials were recorded for each subject except for subject LM for whom 161 trials were lost due to recording errors in session 4. 2287 of 30559 trials (7.5%) were excluded, 847 anticipations (2.8%), 245 blinks (0.8%), 142 fixation errors (0.5%), 775 drift errors (2.5%), and 278 trials (.9%) containing two or more errors simultaneously (figure 12).

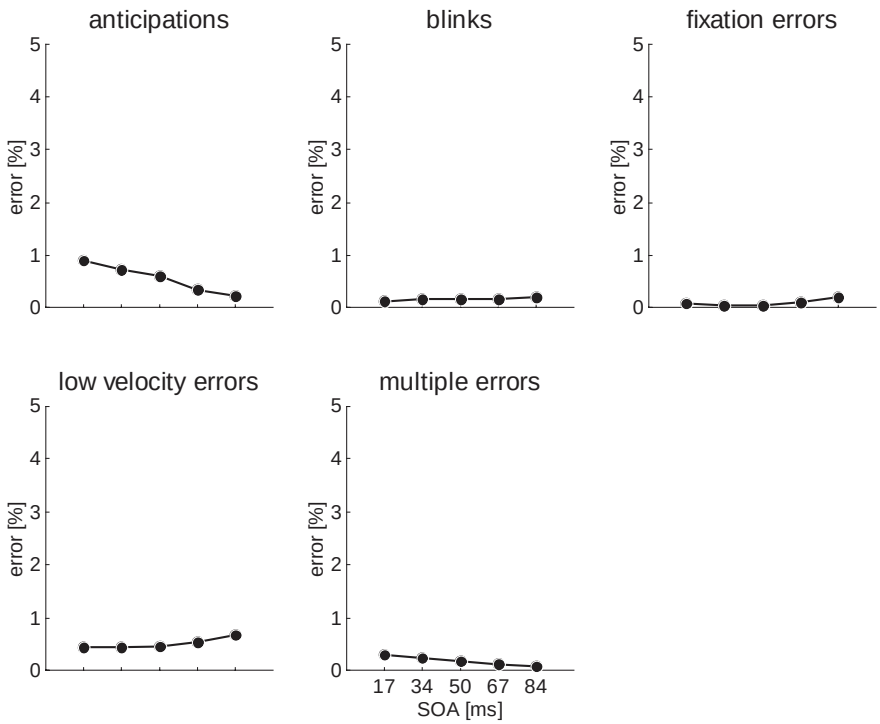


Figure 12: 2284 trials (7.5%) were excluded due to errors. Each panel shows the contribution of different error-types by SOA (see section error handling). Trials in which two or more types of errors occurred were defined as multiple errors.

2.1.2.1 Saccadic reaction time

Mean saccadic reaction time across all conditions was 244 ms (sd = 9.8 ms). Saccadic reaction times differed as a function of congruence and SOA (figure **13**), with shorter reaction times if prime and target were congruent (0°) and longer reaction times if prime and target were maximally incongruent (180°). The effect of congruence was ordered by degree of congruence except for the 180° condition. If primes and targets pointed to opposite directions, reaction times were below those of the 135° congruence condition. Further, the effect of congruence increased with SOA.

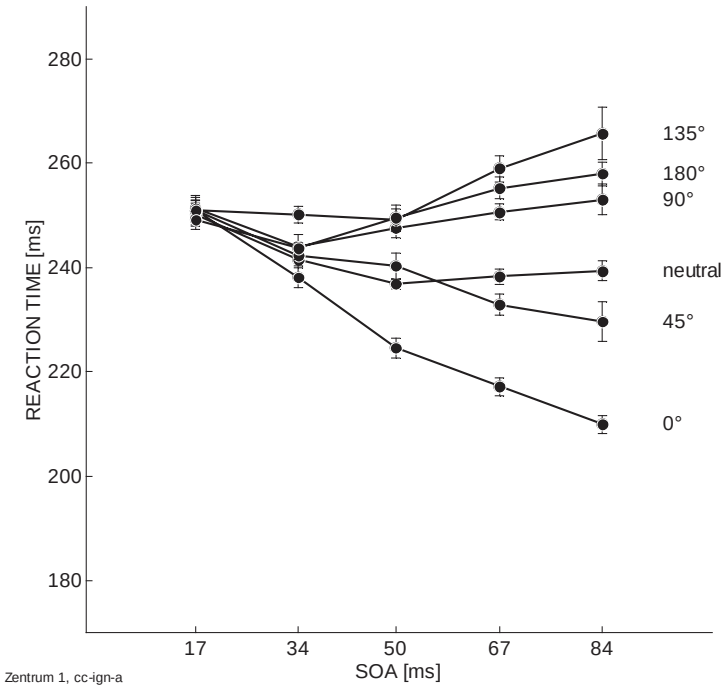


Figure 13: Mean saccadic reaction times for different congruence conditions depending on SOA. Error bars indicate the standard error of mean computed after normalizing interindividual differences (see section error bars below).

To compare these priming effects with the ones obtained by Vorberg et al. in a manual 2AFC task and with the predictions of the accumulator model, the priming effect was computed for each subject as the difference between the maximally incongruent (180°) and the congruent (0°) conditions (figure **14**). The priming effect increased linearly with SOA, leading to a priming function of:

$RT_{180°} - RT_{0°} = .794\ SOA - 16.7$ ms.

Shorter latencies with congruent than with incongruent primes and the linear increase of these priming effects with SOA confirm the predictions of the accumulator model. However, the observed slope of ≈ .8 is outside the model's limits. Additionally, slopes for intermediate congruence levels need explanation.

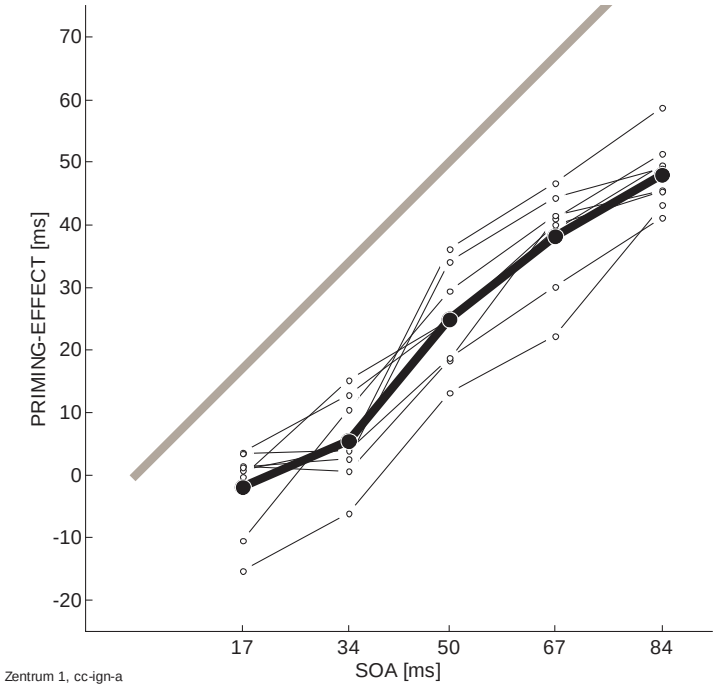


Figure 14: The priming effect is defined by the difference between saccadic reaction times for maximally congruent (0°) trials and maximally incongruent trials (180°). Thin lines with open circles show the data for individual subjects. The priming effect increases linearly with SOA (thick solid line). The gray diagonal shows a theoretical priming effect with unit slope where the priming effect equals SOA.

Statistical analyses. Mean saccadic reaction time was 244 ms (sd = 9.8ms). Statistical analyses were performed by means of Huynh-Feldt corrected analyses of variances (ANOVA) for repeated measures with SOA and congruence as independent variables and saccadic reaction time as the dependent variable. The ANOVA yielded highly significant effects for SOA ($F_{4,28} = 5.73$, $p_{HF} = .025$), congruence ($F_{5,35} = 85.6$; $p_{HF} < .001$) and for the interaction of congruence and SOA ($F_{20,140} = 23.1$; $p_{HF} < .001$). Saccadic reaction time decreased with level of congruence. Adjacent congruence levels differed in their mean reaction times except for 135° vs 180° (0° vs 45°: $F_{1,7} = 54.5$, $p < .001$; 45° vs. 90°: $F_{1,7} = 58.2$, $p < .001$; 90° vs. 135°: $F_{1,7} = 32.1$, $p = .001$; 135° vs. 180°: $F_{1,7} = 4.8$, $p = .064$).

The priming effect ranged from –2 ms at SOA 17 to 48 ms at SOA 84 (-2, 6, 25, 38, and 48 ms). A one-way repeated measures ANOVA with SOA as independent and priming effect as the dependent variable showed a highly significant effect for SOA ($F_{4,28} = 132.2$; $p_{HF} < .001$). Pairwise differences revealed that the priming effect increased with SOA (17ms vs. 34ms: $F_{1,7} = 7.2$, $p = .031$; 34ms vs. 50ms: $F_{1,7} = 43.9$, $p < .001$; 50ms vs. 67ms: $F_{1,7} = 72.3$, $p < .001$; 67ms vs. 84 ms: $F_{1,7} = 25.8$, $p = .001$). A linear regression resulted in a slope of $.794 \pm .049$ for SOA ($t = 16.120$; $p < .001$) and an intercept of -16.7 ms.

Error bars show a within-subject confidence interval (Loftus and Masson, 1994). Reaction times are normalized by subtracting a subject-deviation score from each single data point (here reaction time). The subject-deviation score is the difference of the grand mean (average across conditions and subjects) and the corresponding subject's mean. Standard error of mean is computed with those normalized scores. The confidence interval *CI* for a condition *j* with mean *M* and standard error *se* is: $CI = M_j \pm 2se_j$.

2.1.2.2 Influence on saccade metrics

An eye movement is characterized by its latency with respect to the triggering event, its duration, its starting- and landing position, and by the trajectory describing how the point of gaze moved during the saccade. It has been shown above that saccadic reaction time was systematically influenced by congruence of prime and target. These results could be restricted to decision processes, which determine the onset of the movement but not its programming, but recent electrophysiological and brain imaging studies on masked priming indicate that primes induce a covert motor activation in manual reactions (Dehaene et al., 1998; Leuthold and Kopp, 1998). If this finding applied to ocular responses as well, then covert saccade preparation due to the prime should interfere with response preparation of the overt saccade triggered by the target (Glimcher and Sparks, 1992).

Figure 11 clearly shows that saccade landing positions often deviated from the intended target positions. Two types of deviations will be analyzed separately in the following sections: 1) Deviations in direction and 2) deviations in amplitude.

2.1.2.2.1 Directional deviations of gaze trajectories

If primes gain access to the preparation of motor responses, then saccade metrics in incongruent conditions are especially interesting. In correct trials, the target should almost exclusively trigger the overt response, but primes may have contributed to their response preparation. For that reason it might be possible to observe prime-related components in the overt behavior. If, for example, a prime pointing to the left was followed by a target which pointed upwards, the resulting gaze trajectory and saccade landing position might be shifted towards the direction in which the prime had been pointing.

For the analysis of directional deviations, saccade locked gaze trajectories from the 45, 90, and 135° congruence-levels were rotated and reflected as if the target always pointed upwards, and the prime always pointed into to the left half field (figure 15). The results were amazing. Gaze trajectories deviated from a straight path and most saccades did not land were they where intended to. The most surprising result was that, contrary to the expectations, most deviations were away from the direction to which the prime had been pointing. Only with 135° congruence gaze trajectories deviated towards the marker pointed to by the prime. Gaze deviations were smallest at short SOAs.

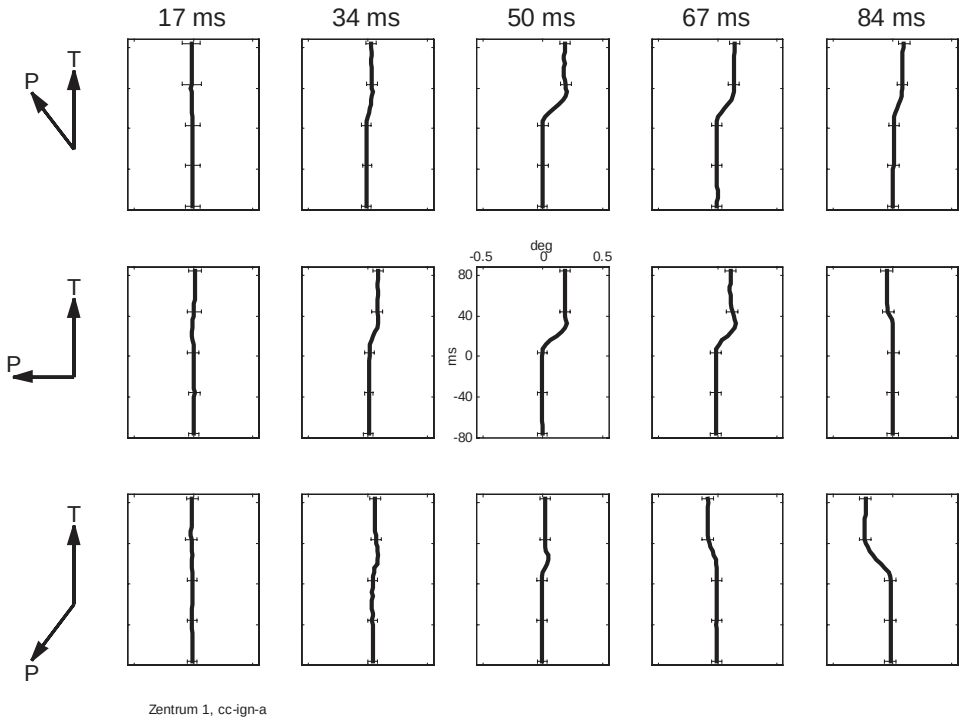


Figure 15: Saccade locked mean deviation of gaze trajectories from a straight path towards the peripheral marker. All trajectories were rotated and reflected as if the target (T) always pointed upwards and the prime (P) always pointed to the left. Each column shows the data for the same SOA between prime and target. Each box shows 80 ms before and after saccade onset (t=0 ms). Error bars indicate within-subject confidence intervals.

For analysis of gaze deviations all saccade locked gaze trajectories were rotated upwards, and additionally reflected in the case that $\phi_{target} - \phi_{prime} > 0°$. This resulted in gaze trajectories for which the target was always pointing upwards and the prime was pointing to left half of the visual field. Each column represents data for the same SOA between prime and target. Each box shows samples from 80 ms before and 80 ms after saccade onset (t=0 ms).

By means of analyzing gaze trajectories it was expected to reveal traces of response preparation. The direction of deviations indicates that the opposite was found, that is response inhibition. Because it is likely that inhibition needs time to build up, it should be possible to distinguish between response preparation and response inhibition by analyzing gaze trajectories in conjunction with response speed. For this purpose, the data were partitioned for each subject under each condition by median split. In these subsets, trajectories differed when SOA was long. Gaze trajectories with early saccade onset deviated towards the marker to which the prime pointed, with late onset, trajectories deviated away from it (figure **16**). Time proved to be a critical factor: Deviations increased with SOA, that is, when more time was available to process the prime. Moreover, deviations depended on saccade latency, with early and late saccade latencies producing distinct deviation-patterns.

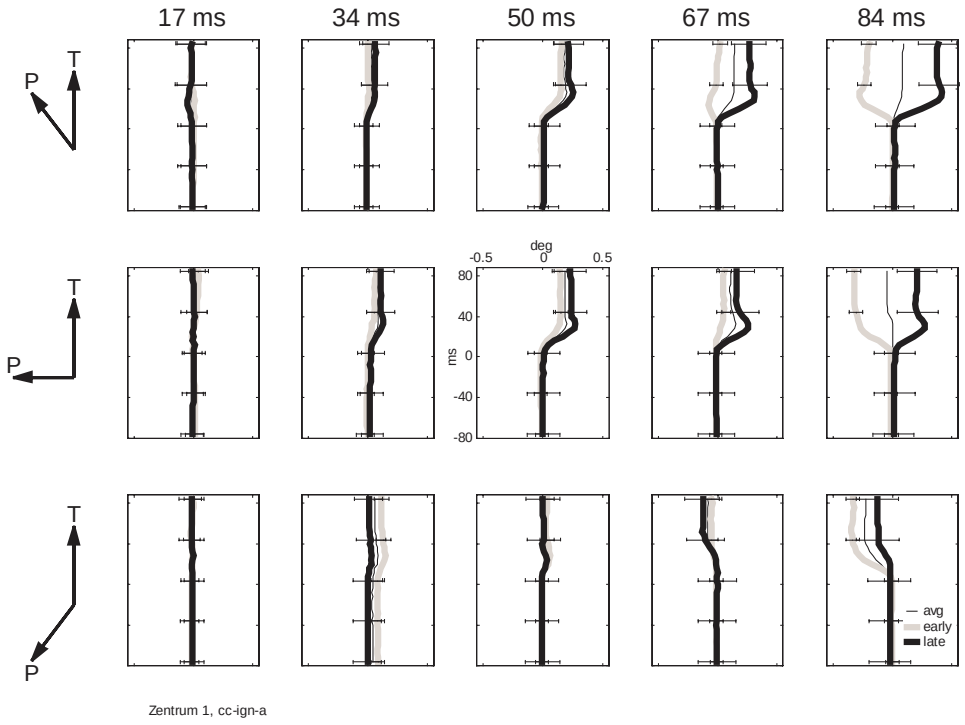


Figure 16: Saccade locked mean deviation of gaze trajectories. Trajectories have been separated by median split of saccadic reaction times into early (grey) and late saccades (black). Thin black lines depict the average gaze trajectories (avg) from figure 15.

2.1.2.2.2 Saccade amplitude

Saccades to peripheral stimuli typically overshoot when they are small (< 2°), whereas they commonly undershoot with amplitudes above 2.5°. Overshoot and undershoot are quantified by the gain parameter, which is the ratio of desired and performed amplitude. Saccade gain above 1 indicates overshoot; undershoot leads to a gain below 1. Intentional saccades to a visual target with more than 2.5° eccentricity typically have a gain of .9, which means they undershoot by 10% (Becker and Fuchs, 1969).

At the beginning of the results section, it was illustrated in figure 11 that saccade gain varied among the experimental conditions. Can these variations be attributed to systematic influence of prime-target congruence and SOA? The results are shown in figure 17. In the congruent and the neutral conditions there was only a decrease of 2% in gain (from .885 at SOA 17 to .867 at ISI 84 ms). All incongruent conditions produced a strong gain-decrease of 12.5% (from .885 at SOA 17 to .77 at SOA 84 ms). The results indicate that primes actually do induce response preparation that interferes with the overt response triggered by subsequent targets.

From figure 11 it is obvious that saccades towards targets in the lower visual field had a higher gain than those that were directed upwards. This is a common result for normal subjects (Troost et al., 1974). Separate analyses revealed that the effect of half-field was simply additive and did not change the overall data pattern.

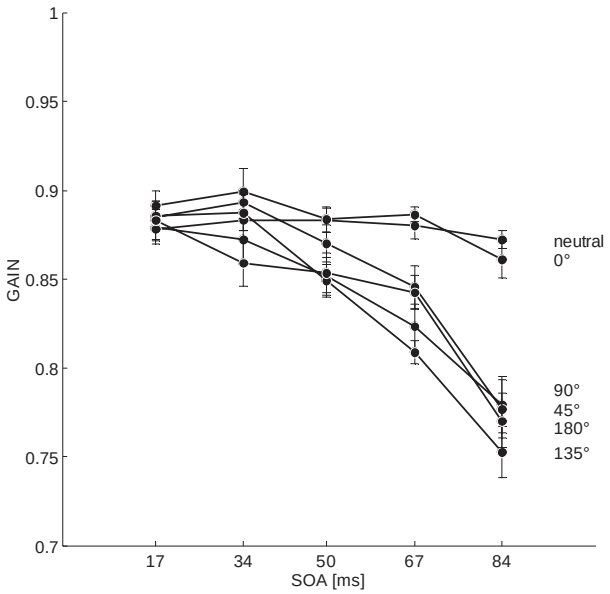


Figure 17: Average gain and normalized error bars as a function of SOA and congruence. Congruent and neutral conditions led to a small decrease of saccade gain only. In incongruent conditions gain decreased with SOA, independent of degree of incongruence.

Statistical analyses. Congruence levels of 45, 90, and 135° were split into those conditions in which the prime appeared counterclockwise with respect to the target ($\phi_{target} - \phi_{prime} < 0°$; congruence = -45, -90, and –135°) and those conditions in which the prime appeared clockwise with respect to the target ($\phi_{target} - \phi_{prime} > 0°$), leading to 9 levels of congruence here. A repeated measures ANOVA with gain as the dependent variable produced significant effects for SOA ($F_{4,28} = 24.3$, $p < .001$), congruence ($F_{8,56} = 9.3$, $p < .001$) and the interaction SOA×congruence ($F_{32,224} = 2.672$, $p < .001$; $p = .045$). Contrasts revealed that the significant interaction was due to gain differences between the neutral and the congruent conditions on the one hand and the incongruent conditions on the other hand ($F_{1,7} = 29.9$, $p = .001$). Gain did not differ in the neutral and the congruent condition ($F_{1,7} = 1.24$, $p = .302$). The congruent and the neutral conditions alone did not influence saccade gain. An ANOVA on congruent and neutral conditions only, produced a main effect for SOA ($F_{4,28} = 2.96$, $p = .037$), but it failed to detect any differences for congruence ($F_{1,7} = 1.24$, $p = .302$) or the interaction of SOA and congruence ($F_{4,28} = .889$, $p_{HF} = .484$).

In incongruent conditions, saccade gain decreased uniformly with SOA. An ANOVA on the incongruent conditions only, showed a significant main effect for SOA ($F_{4,28} = 25.5$, $p < .001$), but failed to produce a main effect for congruence ($F_{4,28} = 2.31$, $p_{HF} = .051$) or the interaction ($F_{24,168} = 1.023$, $p_{HF} = .436$). There were no differences between corresponding congruencies (-135° vs. 135°: $F_{1,7} = .03$, $p = .861$; -90° vs. 90°: $F_{1,7} = .06$, $p = .813$; -45° vs. 45°: $F_{1,7} = 3.96$, $p = .87$), which allows to collapse over negative and positive levels of corresponding congruencies as shown in figure 17. The same analyses were performed separately for saccades towards the upper and the lower visual half-field, respectively. All analyses led to similar effects as in the ANOVAs described above and are therefore not reported.

2.1.2.3 Saccade velocity

Saccade amplitude is determined by the shape of the velocity profile. The critical parameters are saccade duration and the time course of saccade velocity. Analyzing the velocity profiles will allow determining, whether the effect of primes on saccadic gain was due to the primes' effect on saccade duration, saccade peak velocity, or both parameters.

Velocity profiles (figure 18) for saccades under different congruence levels did not change with SOA levels between 17 and 50 ms. Longer SOAs had systematic effects on the velocity profiles for the incongruent conditions only: Saccade duration decreased minimally, although significantly, from 53 to 50 ms in all experimental conditions except for neutral primes. Velocity profiles flattened in the incongruent conditions. Taken together with the observations of gain-decrease reported above, it can be concluded that incongruent primes decrease saccade peak velocity but do not substantially change saccade duration. As in saccadic reaction times, the effect increased with the amount of time, which was available for processing the prime.

With SOA = 84 ms the velocity profiles in incongruent conditions were ordered, with antagonistic primes (180°) producing the highest and congruence of 135° the lowest peak velocities. Again, as in saccadic reaction times, antagonistic primes turned out as an exception: They produced shorter reaction times and higher peak velocities than one would expect from the order of the other congruence levels.

Statistical analysis of velocity was performed with peak velocity (figure 19) as the indicator of saccade kinematics (Becker, 1989) instead of analyzing the dynamic velocity signal. The analysis of saccade peak velocity paralleled the analysis of gain reported above: Congruent and neutral primes did not produce changes in peak velocity over SOA, whereas incongruent primes led to a substantial decrease in peak velocity from 245°/s at SOA 17 ms to 225°/s at SOA 84 ms. The order of incongruent conditions, which was apparent in the velocity profiles, was not confirmed for peak velocity. Saccade peak velocity did not differ among the incongruent levels of priming.

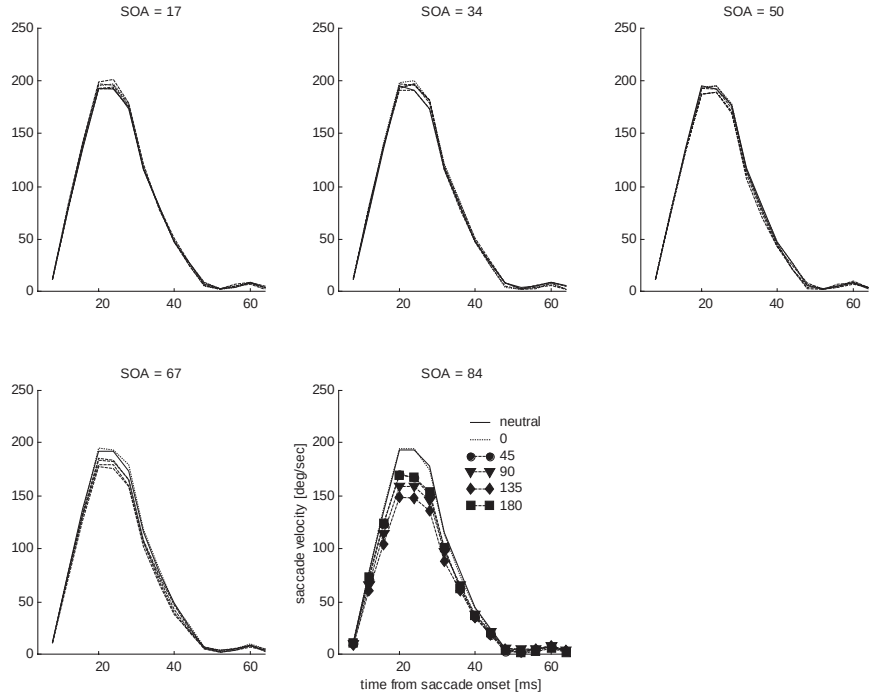


Figure 18: Averaged velocity profiles as a function of SOA and congruence. Velocity profiles did not change in neutral and congruent conditions. In incongruent conditions velocity profiles were flattened with long SOA. Antagonistic primes produced the highest velocities among incongruent conditions.

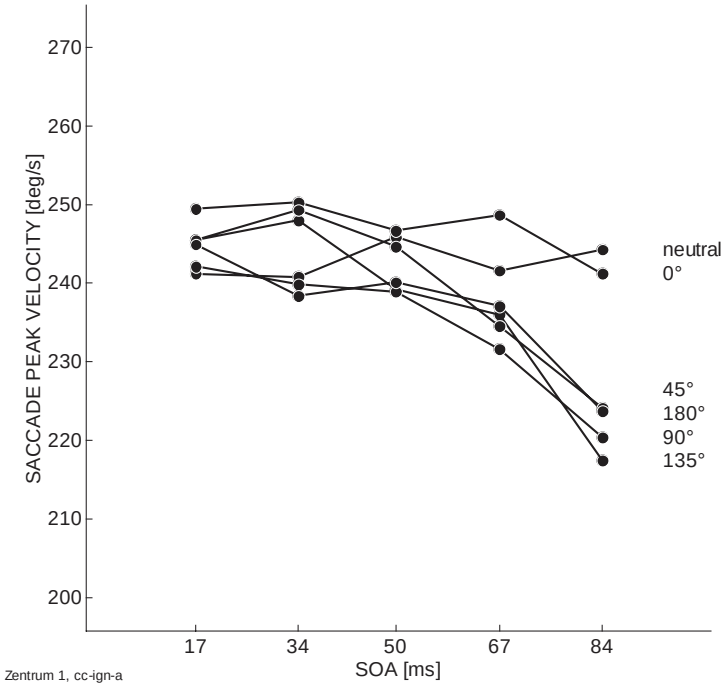


Figure 19: Mean saccade peak velocity remained constant over SOA in neutral and congruent trials, but decreased over time in incongruent conditions.

Statistical analyses.

Velocity: Analysis of variance of saccade peak velocity with SOA and congruence as repeated measures factors (see figure 19) confirmed that saccades became slower with SOA ($F_{4, 28} = 12$; $p_{HF} = .002$). Peak velocity varied with congruence ($F_{5,35} = 7.8$, $p_{HF} = .001$). SOA and congruence interacted ($F_{20,140} = 4.4$, $p_{HF} = .001$). The effect of SOA and the interaction between SOA and congruence are due to the incongruent conditions only. A repeated measure ANOVA with SOA and congruence as factors with neutral and congruent as congruence levels failed to produce any significant effect. Peak velocity remained constant when prime and target are not incongruent (congruence: $F_{1,7} = 4.9$, $p = 0.063$; SOA: $F_{4,28} = .532$, $p_{HF} = .680$; SOA*congruence: $F_{4,28} = 1.649$, $p_{HF} = .208$).

Saccade peak velocities in incongruent conditions were not different from each other. An further ANOVA of the incongruent conditions only showed no effects of congruence ($F_{3,21} = 1.166$, $p_{HF} = 0.336$) and no significant interaction between congruence and SOA ($F_{12,84} = 1.056$, $p_{HF} = 0.401$).

Duration: Duration decreased uniformly with SOA, except for the neutral condition. An ANOVA of duration produced a significant main effect for SOA ($F_{4,28} = 11.8$, $p_{HF} < .001$), and no significant effect for congruence ($F_{5,35} = 2.1$, $p_{HF} = .14$) but for the interaction ($F_{20,140} = 4.5$, $p_{HF} = .041$). Excluding the neutral condition from a further ANOVA eliminated the interaction of SOA and congruence ($F_{16,112} = 1.18$, $p_{HF} = .299$).

2.1.3 Discussion

2.1.3.1 Reaction time effects

The results show that, in addition to manual 2AFC tasks, priming also occurs with ocular responses and in situations with more than two response alternatives. The observed priming effect increased linearly as predicted by the accumulator model. Reaction times were ordered by congruence, with higher congruence leading to shorter reaction times, except for the 180° condition in which reaction times were shorter than in the 135° condition (figure 13). The priming effect $RT_{180°}$ - $RT_{0°}$ had a slope of about 0.8, which is below the lower limit for priming effects predicted by the accumulator model (figure 14).

The observed reaction time functions call for an extension of the accumulator model: When movement direction is subject to priming, the latter is an ordered function of congruence of primes and targets. A formalization about how the degree of congruence should be treated in the accumulator model is given later in the modeling section. Whether degree of congruence has the same effect on other response dimensions than direction, has yet to be determined.

The observed slope of the priming function is a problem for the accumulator model, which needs further elaboration. The accumulator model contains two central claims: 1) accumulators obey saturation, and 2) primes and targets are processed identically. If both conditions are met, variations of saturation cannot account for priming effects with slopes outside 1 and 2 SOA. If processing rate for primes were lower than for targets, a slope below 1 could result, depending on saturation. However, it would be premature to conclude that the postulate of identical processing of primes and masks does not hold, before the specifics of the present task are not understood.

The presence of multiple response alternatives may have introduced additional processes next to accumulation: Regarding the order of the reaction time effects at different levels of congruence, it is obvious that the order is violated by the 180° condition, which has produced shorter reaction times than the 135° condition. Taken together with the observation of $RT_{180°}$ - $RT_{0°}$ being smaller than predicted by the accumulator model, this suggests that antagonistic primes have been treated in a different way than other primes. Yet, it is quite unlikely that antagonistic primes were processed with a lower rate, because this would have required a priori knowledge about congruence. An alternative view is that, after the target has been presented, an inhibitory process altered the representation of primes, and that inhibition was different for different levels of congruence. The assumption of inhibitory processes is in line with the analysis of gaze deviations.

2.1.3.2 Gaze deviations

The rationale of analyzing gaze trajectories was to identify traces of prime-related response preparation. However, the direction of gaze deviations was contrary to what would have been expected. Trajectories deviated to the opposite direction to which the prime had been pointing (figure 15). Examination of gaze trajectories in conjunction with response speed revealed that saccades with early onsets deviated towards the mark to which the prime pointed, and those with late onsets away from it (figure 16). Deviation increased with SOA. The observed data pattern is compatible with the assumption that saccades with early onsets exposed traces of prime-related response preparation whereas saccades with late onsets disclosed the effects of prime suppression. Prime suppression in incongruent trials might serve the purpose of accurate response selection: If an incongruent prime gained behavioral control, a fixation error would occur. For that reason, response tendencies generated by the prime, might be automatically suppressed.

Deviations opposite to the movement direction prepared by the prime may be a sign of an overshooting prime suppression. It may seem puzzling, though, why suppression of prime-related response preparation occurred with congruencies of 45 and 90, but not with 135°. In the 135° condition there were only weak signs for such suppression, with gaze deviations directed towards the orientation of the prime (figures 15 and 16). This suggests that, with respect to the target direction, suppression is strongest if primes have prepared similar response tendencies.

The hypothesis of response suppression is compatible with the analyses of saccade gain and velocity. Incongruent primes produced saccades with smaller amplitudes and flattened velocity profiles. This effect increased as a function of SOA, indicating that suppression took time. Data on saccade gain and velocity profiles paralleled the finding for reaction times: The 180° was neither the slowest, nor the one with least amplitude, and even had the highest velocity profile among incongruent conditions. The data indicate that primes which pointed to locations near to the target location suffered more inhibition than those primes which pointed farther away. Possibly, response suppression is less effective in choice reactions with only two (antagonistic) responses, but becomes more evident when finer-grained responses are required.

2.1.3.3 Conclusion

The accumulator model can generally account for priming effects of eye movements with multiple response alternatives. The model has to be extended in a way, which enables it to represent the similarity of different movement directions. Deviations of gaze in direction and amplitude indicate that priming did not only affect latencies of decision processes, but that primes had direct access to the specification of motor parameters. Further, it is likely that inhibitory processes, as suppression of prime related activity, altered reaction times in a way not accounted for by the accumulator model. The accumulator model has to be extended with a mechanism for suppression, which takes into account the similarity between prime and target.

2.2 Experiment 2: The effect of prime validity on saccadic reaction time and deviation

In this experiment the validity of the prime is increased. Higher prime validity generally has a decreasing effect on reaction times. The rationale behind this experimental variation is as follows. In the previous experiment response inhibition was found in saccades with relatively late onset. Shifting the reaction time distribution towards faster saccades should leave less time for the build up of inhibition. This should produce more fixation errors than in experiment 1, and it should further affect the gaze trajectories which are now expected to deviate towards the prime.

2.2.1 Materials and methods

Figure 20: Neutral prime used in experiment 2.

Equipment, stimuli, procedure and the task were the same as is in experiment 1 with the exception that a neutral prime was used, which contained the critical directional features of all target stimuli (fig. 20). Instead of containing no arrow, the neutral prime simultaneously pointed to each peripheral mark.

Subjects. Three female and two male subjects (mean age 28.2, ranging from 21 to 41 years) with normal or corrected to normal vision participated in 3 1-hr sessions within two weeks. Each subject completed 2256 trials. One subject was paid 10.- DM per hour. Two subjects, among them the author, had already taken part in experiment 1, the remaining subjects were naive to the purpose of the experiment.

Design. In contrast to experiment 1 there were six SOA levels (0, 17, 33, 50, 67, 83, and 100 ms). Nine levels of congruence were used (neutral, 0, -45, +45, -90, +90, -135, +135, and 180°). The critical difference was the relative frequency of congruent and incongruent trials. 50 per cent of all trials were congruent, each of the other eight congruence conditions comprised 6.25 per cent of the trials. As in experiment 1 congruence will be reported as absolute congruence, by collapsing over positive and negative congruence levels. Relative frequency for congruence then is .5 for congruent, .0625 for neutral and 180° and .125 for 45, 90, and 135°.

2.2.2 Results

2.2.2.1 Errors

1145 of 11472 trials (10%) were excluded: 65 anticipations (.6%), 89 blinks (.8%), 867 fixation errors (7.6%), 92 low velocity trials (.8%), and 36 trials containing two or more types of errors (.3%) (see figure 21). In this experiment 75% percent of all errors were fixation errors. Their frequency increased with SOA as predicted by the accumulator model. Such an error pattern suggests that fixation errors responses were triggered by the prime.

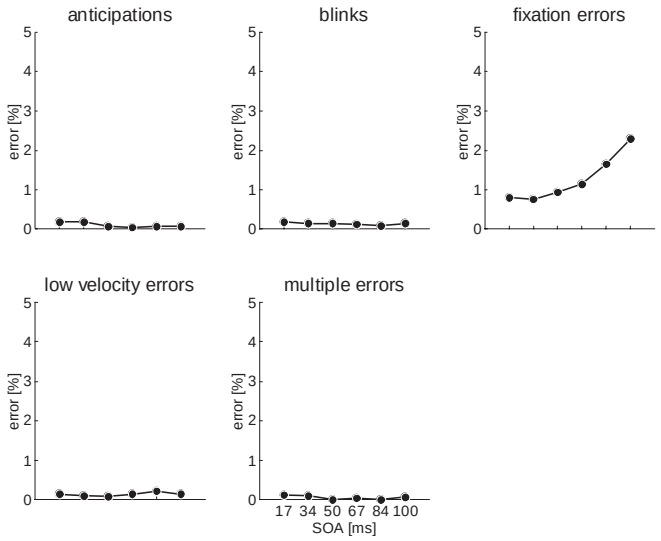


Figure 21: Percentage of different error types by SOA. While probability was constantly low for all other error types, the incidence of fixation errors increased with SOA.

Separate analysis of fixation errors showed that the probability to fixate the wrong position was higher with incongruent than with congruent or neutral primes. Probability of fixation errors increased with SOA for incongruent primes, only. Response preparation to near distractor locations produced more fixation errors than to far distractor locations. Among incongruent primes the probability of a fixation error was highest with primes that pointed next to the target location, and lowest if the prime pointed to the opposite direction. Probability was computed with consideration of the relative frequencies of different congruence levels.

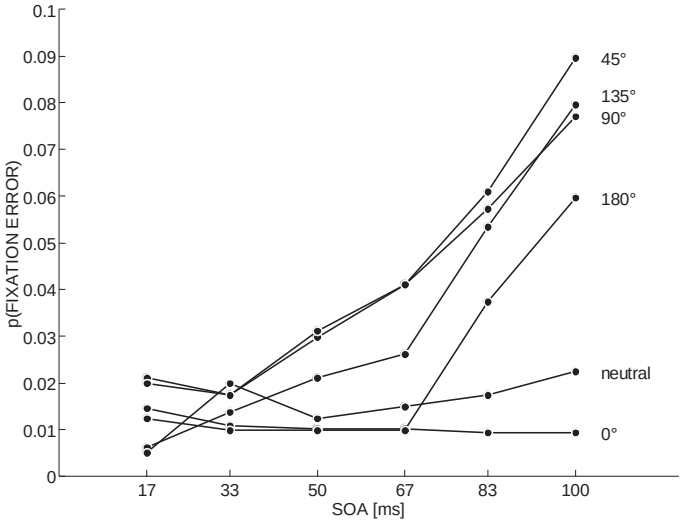


Figure 22: Relative contribution of different congruence levels to fixation errors. Error probability increased as a function of SOA for incongruent primes, only.

Increasing prime validity in experiment 2 also increased error rates. This result is predicted by the accumulator model under the assumption that due to higher reliability of the prime the internal threshold for saccade initiation was lowered. If the threshold-assumption is correct, shorter saccadic reaction times are expected in experiment two compared to experiment 1.

2.2.2.2 Saccadic reaction time

Mean saccadic reaction time across all conditions was almost 30 ms shorter in the present experiment (216 ms, sd = 14.6ms) than in experiment 1 (244 ms, sd = 9.8 ms) while the pattern of reaction time functions remained. Figure 23 shows the mean RTs for correct responses for different levels of congruence as a function of SOA. Congruent primes gave rise to shorter reaction times than incongruent primes. Reaction time effects were, as in experiment1, ordered by congruence with the same exception, that primes pointing in the opposite direction of the target produced faster reaction times than those primes, which pointed only 135° away from it.

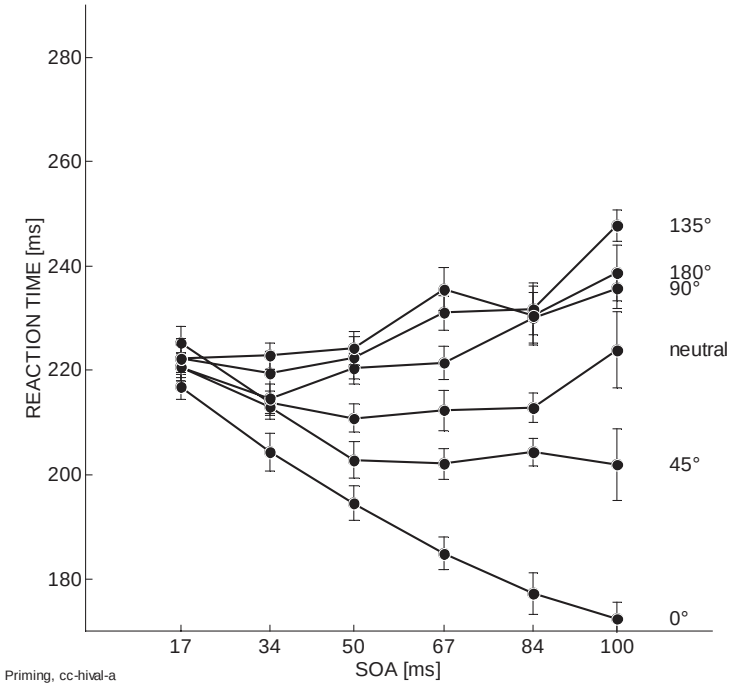


Figure 23: Mean saccadic reaction times for different congruence conditions depending on SOA. Congruence below 90° led to decreasing saccadic reaction times, whereas congruence of 90° and higher led to increasing reaction times at higher SOA.

If the observed shorter reaction times were due to a lowered threshold, then the priming effect should be of comparable size to the one observed in experiment 1. This prediction is based on the analysis of Vorberg et al. (in prep.) that priming effects in the accumulator model are insensitive to rate and threshold variations. As predicted by the accumulator model the priming effect RT180° - RT0° increased linearly with SOA (figure 24). The priming effect has a slope of .738 ± .182, which is significantly below unit slope, but not different from the slope observed in experiment 1 (figure 14).

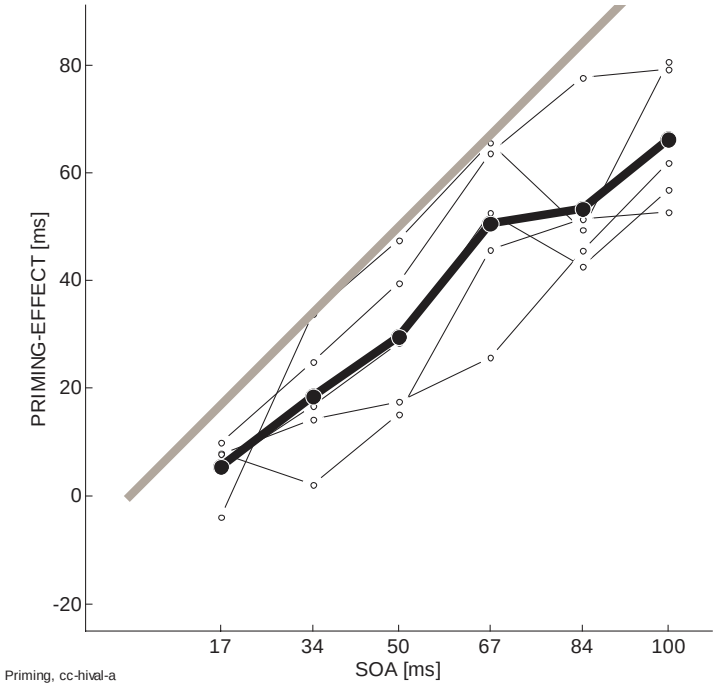


Figure 24: The priming effect increased linearly as a function of SOA. Thin lines with open circles show the data for each individual subject. The gray diagonal shows a theoretical priming effect with unit slope.

Statistical analyses. A repeated measures ANOVA yielded highly significant effects for congruence ($F_{5,20}$ = 48.1; p_{HF} < .001) and for the interaction congruence×SOA ($F_{25,100}$ = 10.8; p_{HF} < .001) but no effect of SOA ($F_{5,20}$ = 2.7, p_{HF} = .096).

Saccadic reaction time decreased with level of congruence. Pairwise contrasts of adjacent congruence levels were significant except for 135° vs. 180° (0° vs. 45°: $F_{1,4}$ = 34.8, p = .004; 45° vs. 90°: $F_{1,4}$ = 37.4, p = .004; 90° vs. 135°: $F_{1,4}$ = 4, p = .117; 135° vs. 180°: $F_{1,4}$ = .008, p = .934).

The priming effect (*pe* = $RT_{180°}$-$RT_{0°}$) was highly significant ($F_{5,20}$ = 30.1; p < .001). The effect ranged from 6 ms at SOA 17 ms to 66 ms at SOA 100 ms. A highly significant linear trend was found for SOA ($F_{1,4}$ = 167.2, p < .001) although not all adjacent SOA differed from each other (17 ms vs. 33 ms: $F_{1,4}$ = 3.3, p = .144; 33 ms vs. 50 ms: $F_{1,4}$ = 30.9, p = .005; 50 ms vs. 67 ms: $F_{1,4}$ = 31.1, p = .005; 67 ms vs. 83 ms: $F_{1,4}$ = .151, p = .717; 83 ms vs. 100 ms: $F_{1,4}$ = 5.5, p = .079). A linear regression resulted in a slope of .738 ± .162 for SOA (t = 9.3; p < .001) and an intercept of –6 ms.

2.2.2.3 Influence on saccade metrics

Gaze deviations observed in experiment 1 were interpreted as signs of response inhibition, because they deviated away from the location to which the prime had pointed. Separate analysis of gaze trajectories for saccades with early vs. late onset revealed that saccades with early onset deviated towards the location to which the prime had pointed whereas trajectories with late saccade onset deviated away from it. This finding suggested that response inhibition takes time. Saccade latencies in the present experiment were found to be about 30 ms shorter than in experiment 1. Consequently, less signs of response inhibition of incongruent primes should be observed, and gaze trajectories should deviate in the direction of the location to which the prime was pointing.

2.2.2.3.1 Saccade landing positions and gaze trajectories

Saccade locked gaze deviations for congruence levels 45, 90, and 135° are shown in figure 25 as a function of SOA. Deviations were towards the location to which the prime was pointing and increased with SOA. The observations confirm the assumption that primes have access to the specification of response parameters and that response preparation and response inhibition can be distinguished by the direction of gaze deviations.

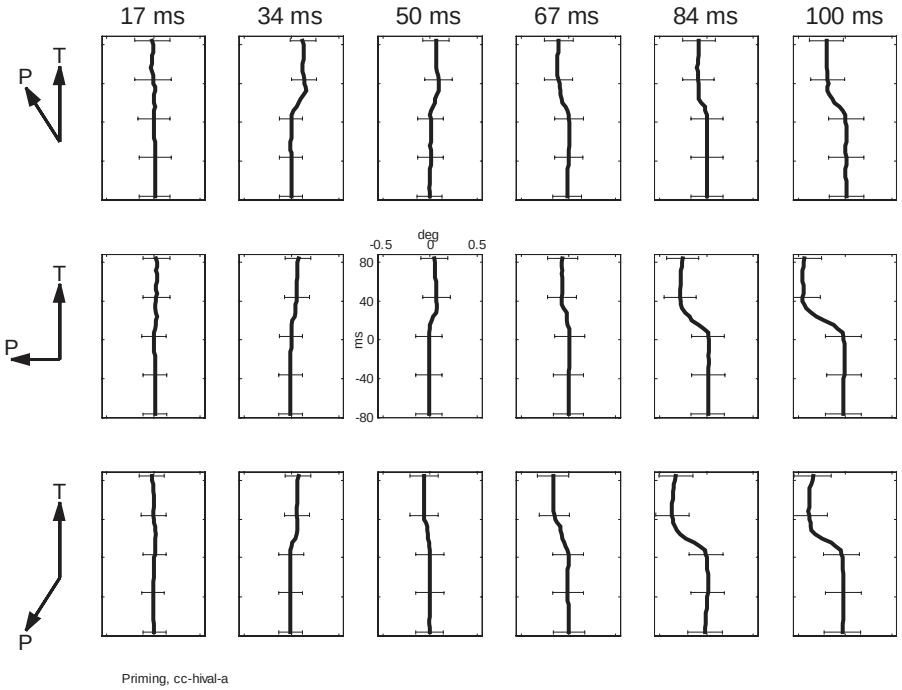


Figure 25: Saccade-locked mean deviation of gaze trajectories as a function of congruence and SOA. Error bars indicate confidence intervals.

Trajectories of early and late saccades showed a similar pattern with deviations of comparable size to those observed in experiment (figure 16). However, early and late effects were not distinguishable due to lack of statistical power.

Different congruence conditions produced different patterns of deviations. A repeated measures ANOVA of deviation of saccade landing position produced a marginal main effect of congruence ($F_{5,20} = 2.7$, $p = .051$) and a significant effect for SOA ($F_{5,20} = 6.9$, $p_{HF} = .03$) and for the interaction ($F_{25,100} = 3.0$, $p < .001$, $p_{HF} = .006$). The interaction is due to deviation-differences in conditions, which require a change of saccade angle (i.e. 45, 90, and 135° congruence) vs. those, which require no change (neutral and 0°) or a reverse of angle (180°).

2.2.2.3.2 Saccade amplitude

Saccades in experiment 2 typically undershot. Average gain across conditions was .87, and did not differ from experiment 1 (.85). Gain decreased in incongruent conditions by 9% (from .92 to .81), but in contrast to experiment 1 there gain also decreased in the neutral condition.

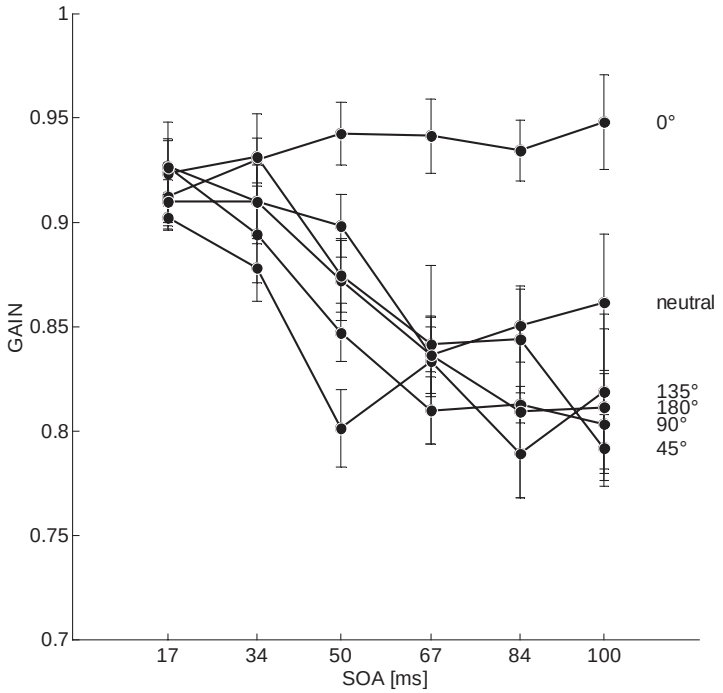


Figure 26: Average gain as a function of SOA and congruence. Gain decreased in the neutral and in incongruent conditions.

Gain of the primary saccade showed a dependency on SOA as well as on congruence (fig.26). A repeated measures ANOVA produced significant effects for SOA ($F_{5,20} = 7.4$, $p_{HF} = .005$), congruence ($F_{8,32} = 5.3$, $p_{HF} < .005$) and the interaction congruence×SOA ($F_{40,60} = 1.6$, $p_{HF} = .028$).

Contrasts revealed that the significant interaction was due to gain differences between the congruent condition on the one hand and the incongruent and neutral conditions on the other hand ($F_{1,4} = 15.1$, $p = .018$). Unlike in experiment 1, gain differed between the neutral and the congruent condition ($F_{1,7} = 15.7$, $p = .017$).

2.2.2.4 Saccade velocity

Saccade duration was about 51 ms in all conditions. Saccade peak velocity was higher than in experiment 1 (259°/s compared to 240°/s). Trajectories had a different velocity profile (figure 27) than that observed in experiment 1 (figure 18), with a dip after 24 ms. Such profiles have already been observed (A. Inhoff, personal communication), but to the authors knowledge not yet been documented or explained.

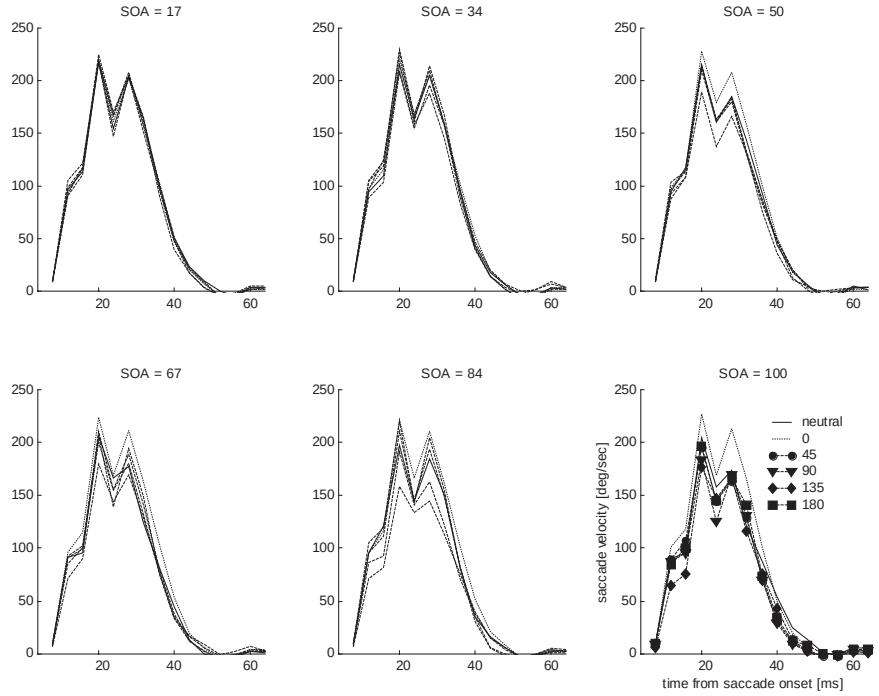


Figure 27: Average velocity profiles as a function of SOA and congruence. All profiles showed a dip of about 40°/s 24 ms after saccade onset.

Velocity profiles for congruent primes were always highest, but separation of congruent and incongruent conditions was not as clear-cut as in experiment 1. However, the analysis of peak velocity showed that incongruent primes did affect saccade velocity. As in experiment 1 peak velocity data paralleled the results for gain. Saccade peak velocity decreased with SOA in incongruent and neutral conditions, but not in the congruent condition (figure 28).

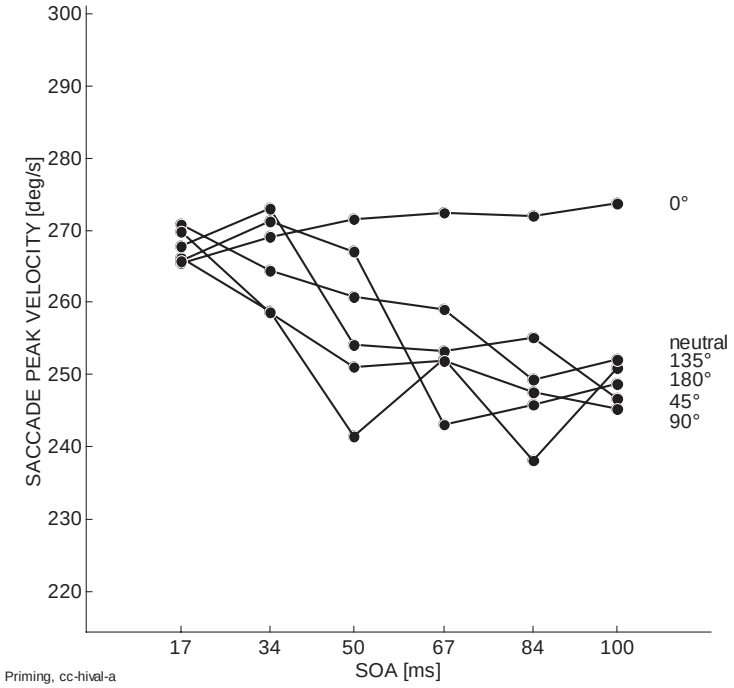


Figure 28: Mean saccade peak velocity remained constant over SOA in congruent trials, but decreased over time in incongruent and neutral trials.

2.2.3 Discussion

In experiment 2 the validity of the prime was increased to 50% compared to 22.2% in the first experiment. Increasing prime validity led to the predicted decrease in reaction times. Mean saccadic reaction time was 216 ms (s = 14.6 ms) compared to 244 ms (s = 9.8 ms) in the first experiment (figures 13 and 23). Next to differences between the sample of subjects who participated in experiments 1 and 2, faster overall reaction times may have occurred due to lower thresholds and higher processing rates, caused by higher prime validity. The predictions of the model for errors and priming effects are identical for lowering thresholds and increasing processing rates. The number of incorrect responses after incongruent primes should increase with SOA; the priming effect should remain unaffected. Error data and priming effects were compatible with the predictions. The number of fixation errors increased in incongruent but not in congruent and neutral conditions. Interestingly, probability of a fixation error was highest when the prime had pointed to a location next to the one to which the target pointed (figure 22).

Priming effects had comparable slopes in both experiments (figures 14 and 24). Saccade velocity was higher in experiment 2 (259°/s) compared to experiment 1(240°/s), which may indicate that validity changed the strength of response preparation. But comparison of data of the two subjects, who took part in both experiments, did not show any differences between peak velocities between the experiments. But velocity profiles were strikingly different (figures 18 and 27). In experiment 2 they consistently showed a dip after 24 ms. The origin of this effect is unclear.

In contrast to experiment 1 a decrease in gain and peak velocity was observed in the neutral condition, which may be due to the fact that the shape of the neutral stimulus was changed. Whereas in experiment 1 the neutral stimulus did not contain any arrows, here, it contained arrows in all eight possible target directions in experiment 2 (see fig. 20). The neutral stimulus may have triggered inhibitory processes for two reasons: 1) because it contained directional features which were incongruent with those of the imperative stimulus, or 2) occasionally one of the eight arrows of the neutral prime gained behavioral control leading most probably (7 of 8) to an incongruent response preparation, which required inhibitory reactions.

Most importantly, prime validity changed the pattern of gaze deviations. In contrast to experiment 1, saccade landing positions and average gaze trajectories deviated towards the direction indicated by the prime. This effect can be explained in at least two different ways. The first account is a strategic one. If primes predict targets poorly, it might be a good strategy to automatically discard the information provided by the prime through inhibiting prime-related activity. If in experiment 2 subjects were able to learn that the prime was a good predictor for the target, and they might have stopped inhibiting primes. The second account is a dynamic one. It assumes that the processes, which suppress prime-related activity, need a certain minimum of time to become effective. In a situation in which responses are speeded up, those inhibitory processes have less or even no time to influence behavior. Both accounts postulate that a lack of inhibition leads to higher prime-related activity at response initiation, which leads to deviations towards the prime.

Saccade peak velocity (see figure 28) became slower with SOA ($F_{5,20} = 4.4$; $p_{HF} = .007$). Congruence and the interaction between SOA and congruence failed to reach statistical significance (congruence: $F_{5,20} = 3.7$, $p_{HF} = .06$; SOA×Congruence: $F_{25,100} = 1.7$, $p_{HF} = .081$).

2.3 Experiment 3: The influence of masked peripheral primes on eye movements

In the first two experiments centrally presented symbolic stimuli served as primes and targets. It was shown that the effect of primes depends on their congruence with the target. The question, which is addressed in the following experiments 3 and 4, is whether the same priming effects can be achieved by spatial cueing.

2.3.1 Materials and methods

The equipment was the same as in experiment 1. In contrast to experiments 1 and 2, the peripheral saccade target markers were ring-shaped with 0.5° diameter. Primes were discs with 0.4° diameter, which fit into the inner cut out of the saccade target markers. **Subjects**. Four subjects (one female, three male) with normal or corrected to normal vision participated in 8 1-hr sessions within two weeks. Two subjects received course credits. Age range was (23-44) years (mean 30 years). Except for the author, who also took part in the previous experiments, subjects were naive to the purpose of the experiment.

Task. As in the experiments before the task was a speeded eight alternatives forced choice reaction to a central target. The peripheral prime appeared for 17 ms and was metacontrast-masked after a variable interstimulus interval by the onset of the markers at 8 peripheral positions. After an unpredictable interval between 0 an 67 ms the target stimulus was presented. Subjects were not informed about the presence of primes and instructed to direct their gaze as fast as possible to the location indicated by the target stimulus.

Design. SOA (17, 33, 50, 67, and 83 ms) and congruence (neutral, 0, 45, 90, 135, and 180°) were varied in a repeated measures design. In neutral trials no cue was presented. Dependent variables were saccadic reaction time and gaze position. Each subject completed eight sessions with 16 replications of each SOA - congruence combination leading to 640 trials for each congruence level and 3840 trials per subject.

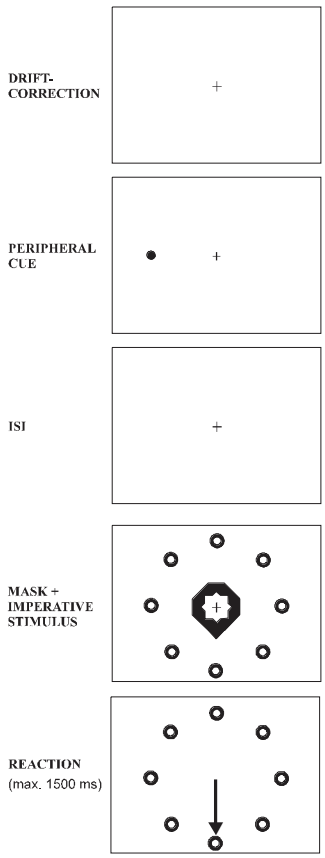


Figure 29: Trial sequence of experiment 3. Subjects started a trial with a key press. After a delay a spatial cue (disc) appeared at one of eight target positions for 17 ms. After a variable SOA (17 to 83 ms) an annulus was presented at each peripheral position which remained until the end of the trial. Annuli served as the masking stimulus for the peripheral cue as well as markers of possible target locations. Simultaneously with mask onset a central imperative stimulus was presented for 50 ms. The subjects' task was to direct their gaze to the target position to which the imperative stimulus pointed. The angle between cue and location indicated by the imperative stimulus varied pseudo-randomly between 0° and 180°.

2.3.2 Results

156 trials of one subject were lost due to recording errors.

2.3.2.1 Errors

793 of 15204 trials (5.2%) were excluded, 208 anticipations or blinks (1.4%), 214 fixation errors (1.4%), 270 low velocity saccades (1.8%), and 101 trials (.7%) containing two or more errors simultaneously.

2.3.2.2 Saccadic reaction time

Mean saccadic reaction time was 218 ms (sd = 3.5ms). Figure 30 shows the mean RTs for correct responses as a function of SOA and congruence. In contrast to previous experiments, incongruent primes did not affect reaction time. Congruent primes led to decreasing reaction times as a function of SOA. Using peripheral cues instead of central primes almost eliminated the linear relationship between priming effect and SOA, which was found in experiments 1 and 2. The priming effect ranged from 1 ms at SOA 17 ms to 16 ms at SOA 83 ms (figure 31). A linear regression resulted in a slope of .207 ± .122 for SOA (t = 3.6; p = .002), which is far below the range of slopes accounted for by the accumulator model, and below the slope priming effects observed with central primes (.794 in experiment 1 and .738 in experiment 2).

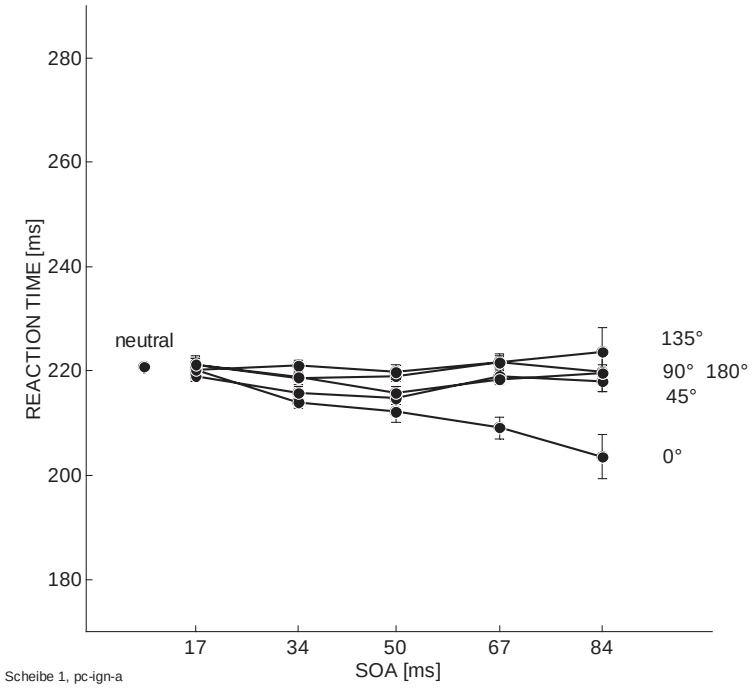


Figure 30: Mean saccadic reaction times as a function of congruence and SOA. Reaction times decreased with congruent cues, but were not affected by incongruent primes.

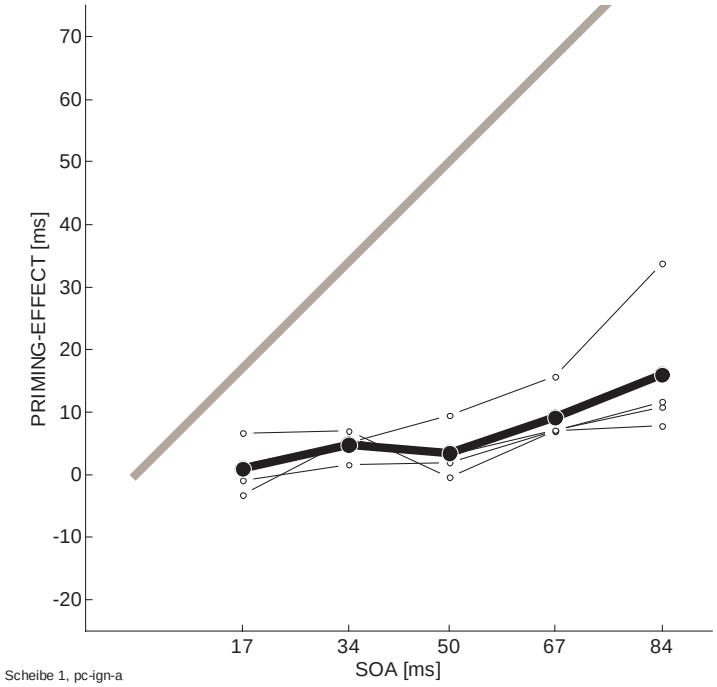


Figure 31: With a slope of .207 (confidence interval = ± .122) the priming effect (*pe* = $RT_{180°}$-$RT_{0°}$) substantially differed from unit slope (gray diagonal). Thin lines show the data for each individual subject.

The neutral condition is excluded from ANOVAs, because, in contrast to previous experiments, no cue or prime was presented here. A two way repeated measures ANOVA yielded a significant effect for congruence ($F_{4,12}$ = 8.7; p_{HF} = .014), but not for SOA ($F_{4,12}$ = 4.4, p_{HF} = .073). There was a significant interaction between SOA and congruence ($F_{16,48}$ = 2.6; p_{HF} = .046). The effect of congruence and the interaction were due to decreasing reaction times for the congruent but not for the incongruent conditions ($F_{1,3}$ = 13.1, p = .036).

A repeated measures ANOVA of the priming effect (figure 31) produced a significant effect for SOA ($F_{4,12}$ = 5.1; p_{HF} = .044). A linear trend for SOA failed to reach significance ($F_{1,3}$ = 5.9, p = .093). A linear regression resulted in a slope of .207 ± .122 for SOA (t = 3.6; p = .002).

2.3.2.3 Influence on saccade metrics

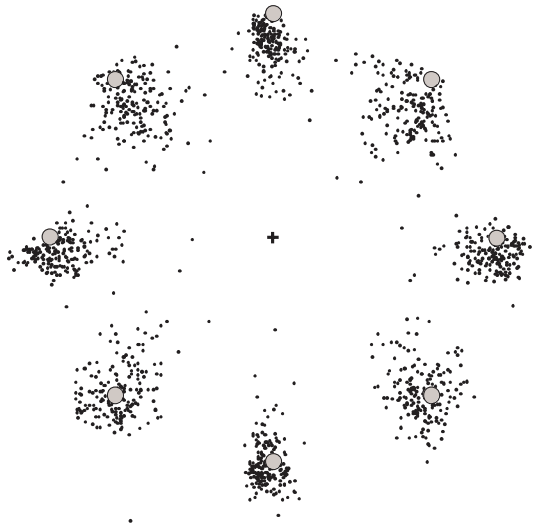


Figure 32: Saccade landing positions for each subject, target position, congruence, and SOA. Although saccade-landing points were more accurate than in experiments 1 and 2, directional and amplitudinal deviations were evident.

Mean saccade-landing positions for all subjects and conditions are shown in figure 32. The figure illustrates that, compared to experiment 1, hypermetric and hypometric saccades did also occur, but that saccades were much more accurate with respect to saccade gain.

2.3.2.3.1 Saccade landing positions and gaze trajectories

SOA and congruence variations did not produce any deviations in mean saccade landing positions or in the average trajectories, but trajectories of saccades with early onsets deviated towards the peripheral prime whereas saccades with late onsets deviated away from the prime. The pattern of gaze deviations in conjunction with response speed was similar to the pattern observed in experiment 1, which also occurred in experiment 2, but was not statistically reliable.

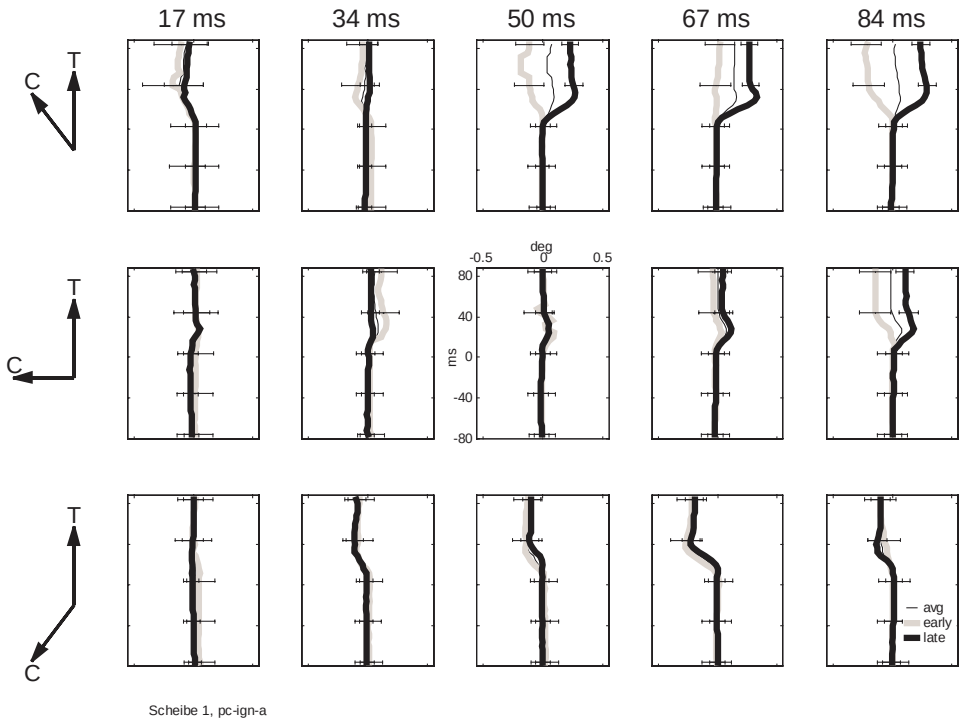


Figure 33: Saccade locked mean deviation of gaze trajectories from an ideal direct path. Eye movements have been separated by median split of saccadic reaction times into early and late saccades. Average gaze trajectories (thin black lines) did not deviate from the ideal path. Saccades with early onset (gray) had trajectories deviating towards the cue, saccades with late onset (thick black trajectories) deviated away from the cue. Error bars indicate confidence intervals.

SOA and congruence variations did not produce any changes in mean saccade landing positions (SOA: $F_{4,12} = .124$, $p = .971$; congruence: $F_{5,15} = .862$, $p = .528$; SOA*congruence: $F_{20,60} = 1.3$, $p = .233$). There were only marginal horizontal deviations from the ideal path in saccade landing positions and in gaze trajectories. However, median split in subpopulations of saccades with early vs. late onset produced gaze deviations towards the cue in all conditions for saccades with early onset and away from the cue in the 45° and the 90° conditions for saccades with late onset (figure 33).

2.3.2.3.2 Saccade gain

Saccade gain was unexpectedly high in this experiment. Average gain across conditions was .95 compared to .85 and .87 in experiments 1 and 2, respectively. Gain was unaffected by congruent primes, but it decreased with incongruent primes (figure 34).

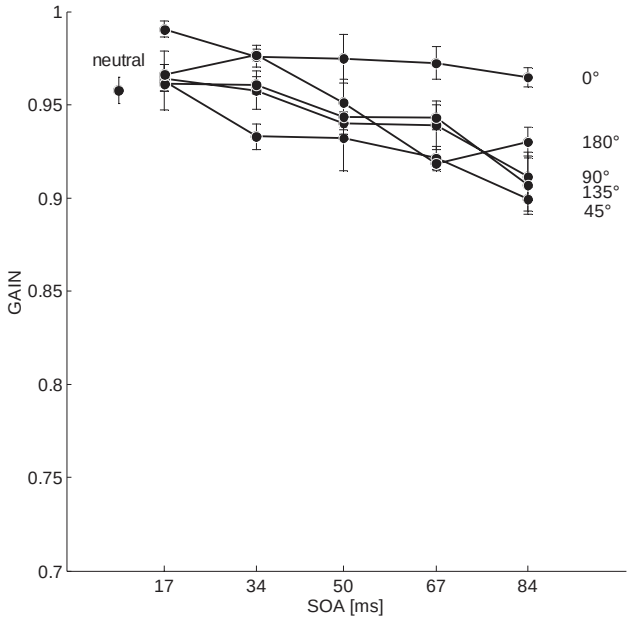


Figure 34: Gain as a function of congruence and SOA. Gain decreased with incongruent primes and was unaffected by congruent primes.

A repeated measures ANOVA produced significant effects for SOA ($F_{4,12} = 35.4$, $p < .001$), congruence ($F_{7,21} = 5.2$, $p = .002$, $p_{HF} = .011$). SOA and congruence did not interact ($F_{32,96} = .81$, $p = .735$; $p_{HF} = .568$).

2.3.2.4 Saccade velocity

Velocity profiles for different congruence levels remained unaffected with congruent primes (figure 35). With longest SOA, incongruent primes produced velocity profiles with peaks 25°/s below the corresponding profile of the congruent condition. Average saccade duration was 54 ms and not influenced by primes.

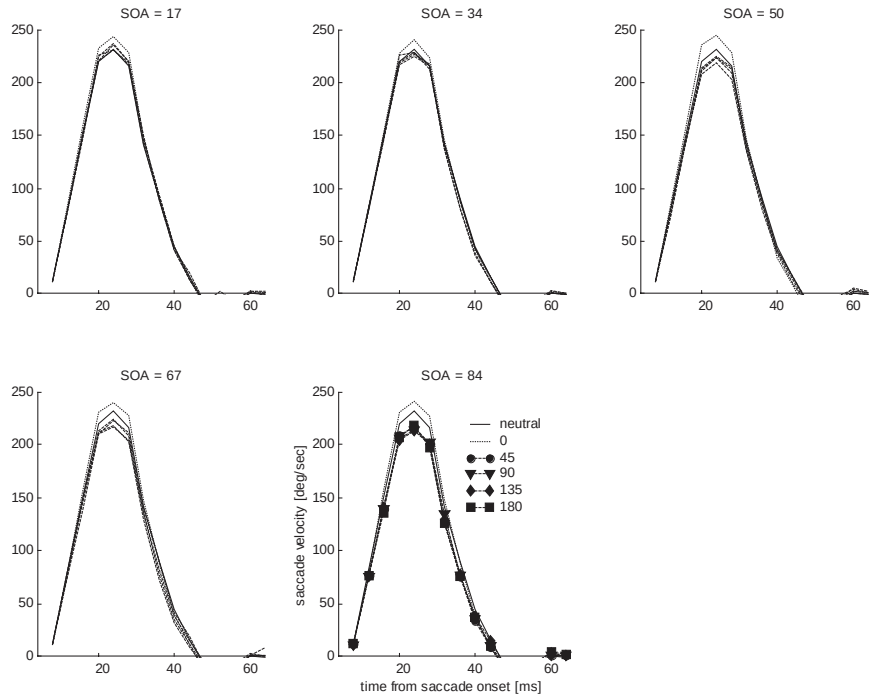


Figure 35: Velocity profiles did not change in the congruent condition. With long SOA, velocity in incongruent condition decreased. Note, that the neutral condition is shown as a reference in all panels, although it was not varied with SOA.

Analysis of variance of saccade peak velocity (see figure 35) revealed that saccades became slower with SOA ($F_{4,12} = 14.0$; $p < .001$, $p_{HF} < .002$). Peak velocity varied with congruence ($F_{4,12} = 6.04$, $p = .007$; $p_{HF} = .008$), due to higher peak velocities in the congruent vs. all other conditions($F_{1,3} = 23.3$, $p = .017$). SOA and congruence did not interact ($F_{16,48} = 1.2$, $p = .286$).

2.3.3 Discussion

Peripheral spatial cues led to substantially smaller reaction time effects upon central imperative stimuli than central primes did. This finding suggests that spatial cueing is fundamentally different from priming with centrally presented symbols. Before discussing the implications of this observation for the accumulator model, a critical objection must be discarded: Maybe peripheral primes were ineffective, because the subjects ignored them. Therefore an additional experiment was performed, in which the behavioral relevance of the cues was increased. The data of the present experiment will be discussed in conjunction with experiment 4.

2.4 Experiment 4: Changing the behavioral relevance of peripheral primes

In the previous experiment a peripheral spatial cue led only to minimal priming effects. Whether these observations were due to fundamentally different processing of central and peripheral primes is uncertain, as long as it is not known whether subjects simply ignored the peripheral prime in experiment 3. In the present experiment primes are task relevant so that subjects cannot fulfill the instructions if they ignore the cue.

2.4.1 Materials and methods

The equipment and stimuli were the same as in experiment 3. In addition, neutral central symbols were introduced to the experiment as imperative stimuli.

Tasks. Two types of tasks were performed throughout the experiment: Priming and cue localization (figure 36). The type of task changed unpredictably from trial to trial, and was announced by the central symbol. A central arrow indicated a priming trial, in which subjects were asked to direct their gaze to the peripheral position to which the arrow was pointing. In the neutral condition no prime was presented. A central symbol, which did not contain an arrow, indicated that prime localization was required. In localization trials subjects were instructed to direct their gaze to the location where the prime was presented. Two thirds of the trials were priming trials; in the remaining third, cue localization was required.

Subjects. Six subjects (3 women, 3 men) with normal or corrected to normal vision participated in 8 1-hr sessions within two weeks. Age range was 21-44 years (mean 27.3 years). Two subjects received course credits. Four subjects were naive to the purpose of the experiment, and two other subjects, among them the author, had participated in two or all of the previous experiments.

Design. Congruence was varied in six levels (neutral, 0, 45, 90, 90, 135, and 180°). The frequency for all congruence levels was the same in priming trials (see experiments 1 and 3). The critical variation was the addition of prime-localization trials, which did not contain neutral primes. The design contained 3840 priming and 1920 localization trials per subject.

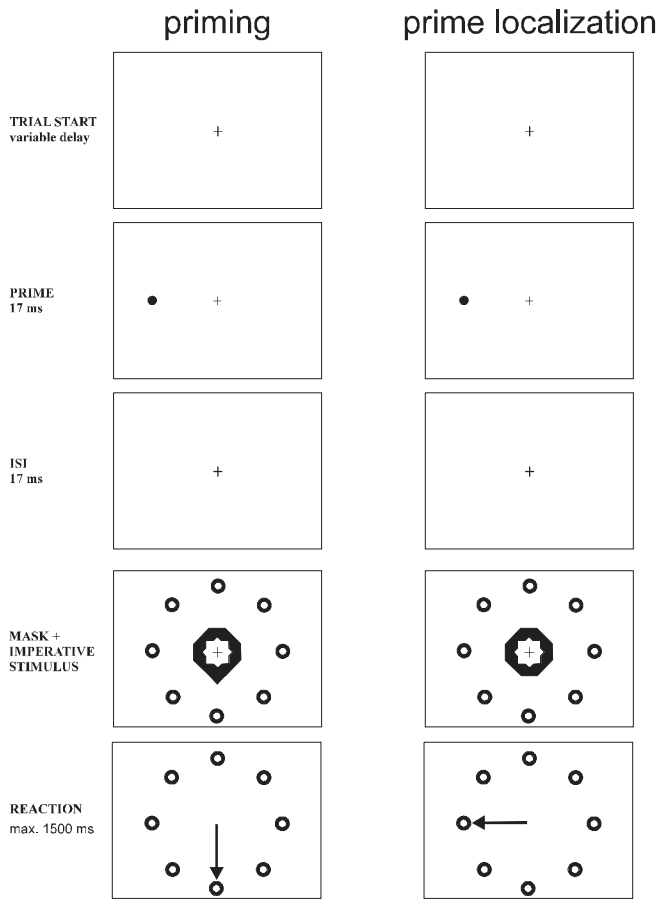


Figure 36: Two thirds of the trials were priming trials (left panel) as described in experiment 3 (see fig. 29). The remaining third of the trials served for prime localization (right panel). A localization trial was indicated by a central symbol, which did not contain an arrow. Subjects were instructed to direct their gaze towards the location of the prime.

2.4.2 Results

Four out of six subjects did not complete the last block of 720 trials (540 priming and 180 localization trials).

2.4.2.1 Cue localization

10560 prime localization trials were performed (four subjects with 1680 and two subjects with 1920 trials). The performance in prime localization was a increased with SOA (figure 37). Primes were correctly localized in 64% with SOA 17 ms to 87% with SOA 84 ms. Chance level was 12.5%. It can be concluded that subjects were paying attention to the primes.

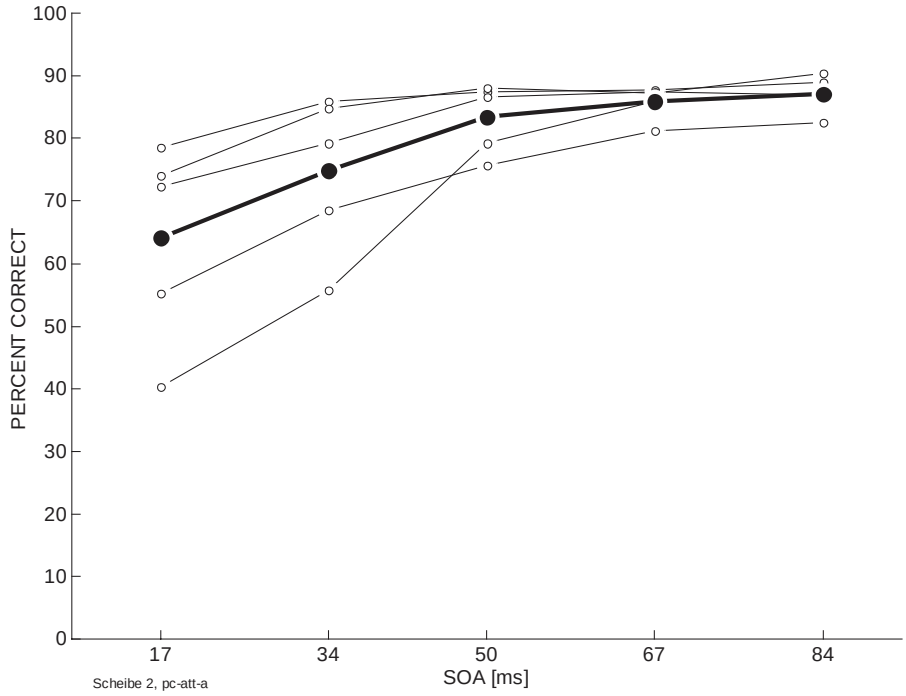


Figure 37: Average performance in prime localization increased with SOA (filled symbols). Thin lines with open circles show the data for each individual subject. Chance level was at 12.5%.

2.4.2.2 Priming

Errors. 22120 priming trials were recorded. 1885 error trials (8.5%) were excluded (418 anticipations, 1.9%; 106 blinks, 0.5%; 875 fixation errors, 4%; 333 drift/low velocity errors, 1.6%; and 160 trials containing two or more types of errors, 0.8%). Increasing the task relevance of primes also increased the probability of fixation errors. As predicted by the accumulator model, the probability of fixation errors rose with SOA (figure 38).

Most errors were of the wrong fixation position type and occurred almost exclusively with incongruent primes (figure 39). Primes next or opposite to the target location produced the majority of fixation errors. This is different from the error pattern in experiment 2 where primes pointing to the opposite direction of the target had the lowest probability among incongruent primes to produce a fixation error (figure 22).

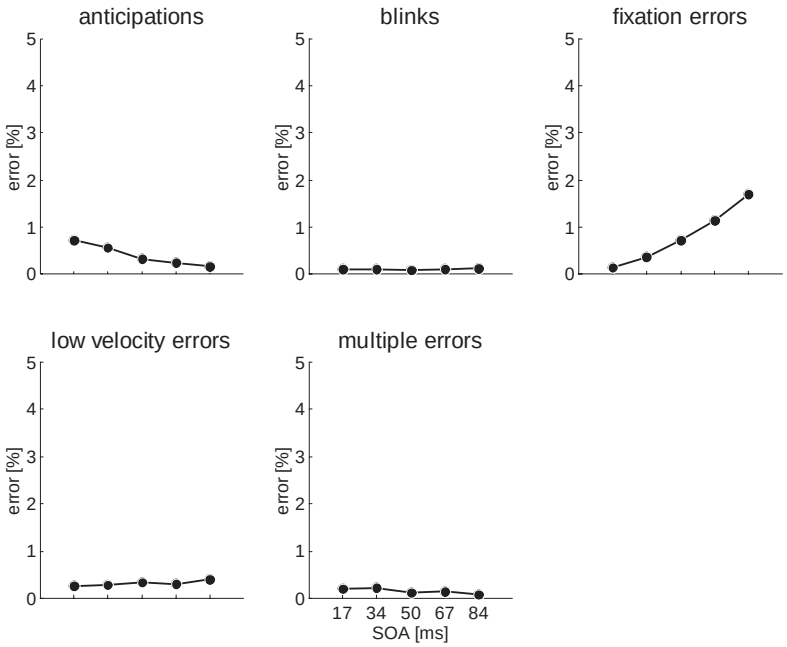


Figure 38: 1885 trials (8.5%) were excluded due to errors. Each panel shows the contribution of different error-types by SOA (see section error handling). Trials in which two or more types of errors occurred were defined as multiple errors.

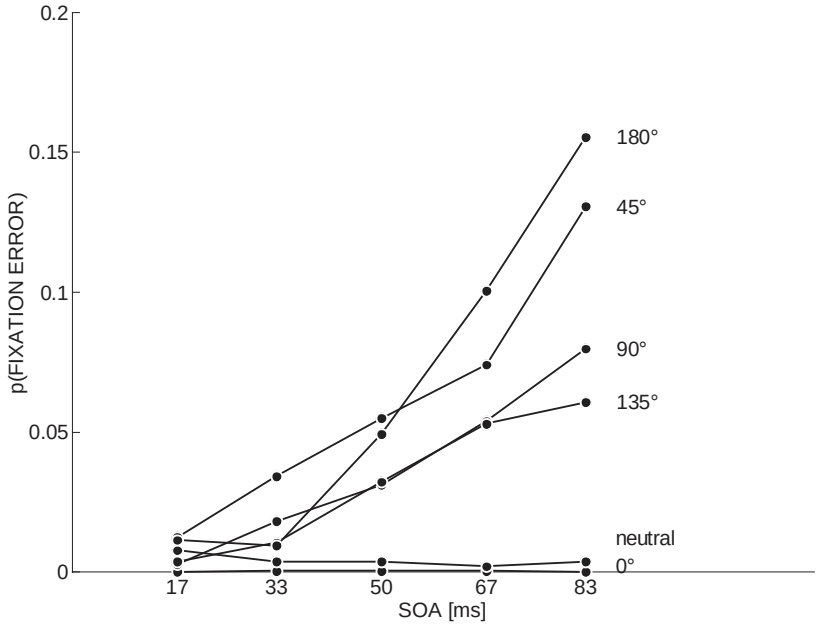


Figure 39: Relative contribution of different congruence levels to fixation errors. Error probability increased as a function of SOA for incongruent primes, only.

2.4.2.3 Saccadic reaction time

Mean saccadic reaction time was 233 ms (sd = 7.4ms). Figure 40 shows that mean RT decreased with congruent and increased with incongruent primes as a function of SOA. Reaction time effects were ordered by congruence. The priming effect increased linearly and was fitted by the function:

$RT_{180°}$-$RT_{0°}$ = 0.274 SOA + 5 ms.

The slope was not different from experiment 3 (.207), but substantially smaller than in experiments 1 (.794) and experiment 2 (.738). The results suggest that peripheral primes have less influence than central primes even in a task in which they are explicitly task relevant.

Statistical analyses. Congruence significantly changed saccadic reaction time ($F_{4,20}$ = 37.9; p < .001), SOA did not produce a main effect ($F_{4,20}$ = .142, p = .965). There was a significant interaction between SOA and congruence ($F_{16,80}$ = 1.97; p = .026, p_{HF} = .103). The priming effect (see figure 41) was subjected to a ANOVA with SOA as the repeated measures factor. It revealed a significant effect ($F_{4,20}$ = 9.4; p < .001, p_{HF} < .008) which had a linear trend ($F_{1,5}$ = 12.5, p = .017). A linear regression resulted in a slope of .274 ± .222 (t = 5.0, p < .001) and an intercept of 5.

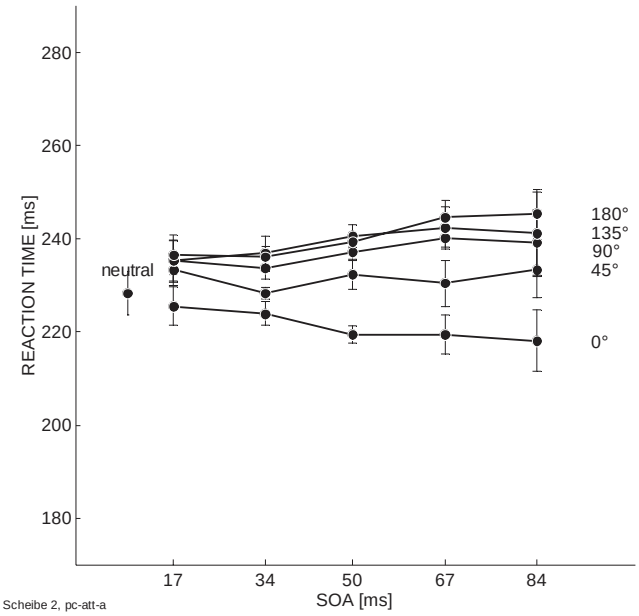


Figure 40: Mean saccadic reaction times for different congruence conditions depending on SOA.

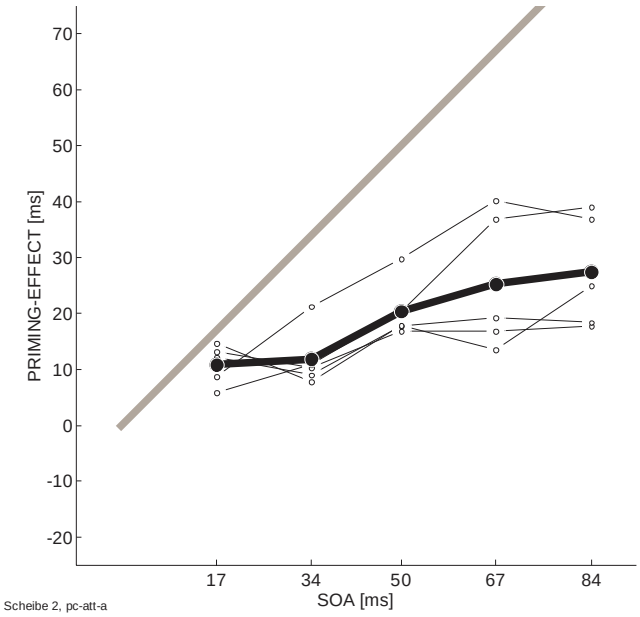


Figure 41: The priming effect increased linearly with a slope of .274 SOA (filled circles). The priming effect substantially differed from unit slope (gray diagonal). Thin lines with open circles show the data for each individual subject.

2.4.2.4 Influence on saccade metrics

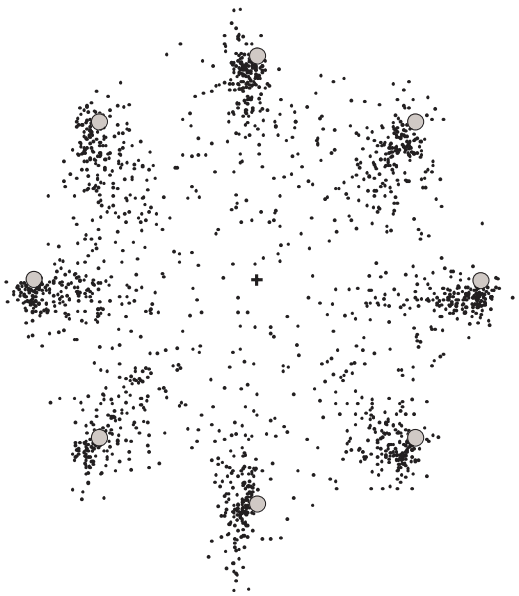


Figure 42: Saccade landing positions for each subject, target position, congruence and SOA.

Saccade landing positions revealed directional and amplitudinal deviations from target locations (figure 42). Remarkably, hypermetric saccades not only occurred towards the lower visual field but also when they were upwards directed.

2.4.2.4.1 Gaze trajectories

Mean gaze trajectories of correct responses deviated towards the primed position under all congruence conditions. Deviations became stronger as a function of SOA (figure 43). Confidence intervals were unusually large and indicated different effects between subjects, which was confirmed by inspection of gaze trajectories separately for each subject (figure 44). Presaccadic confidence intervals were also unusually large, indicating that the peripheral prime induced a presaccadic drift that had not occurred in the previous experiments.

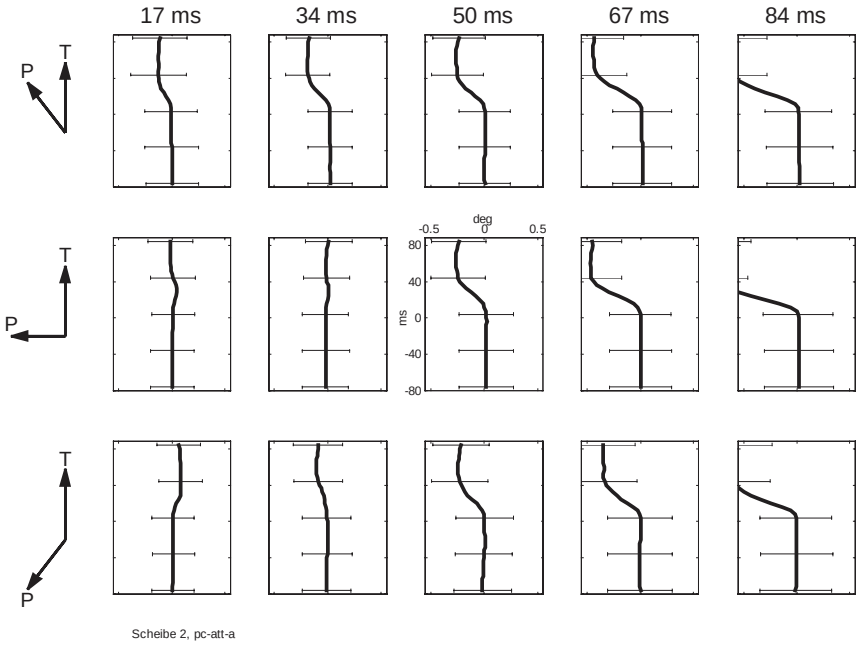


Figure 43: Average saccade locked deviation from a straight path towards the peripheral marker. While landing in close to the target location, trajectories deviated towards the site of the prime. Error bars indicate confidence intervals.

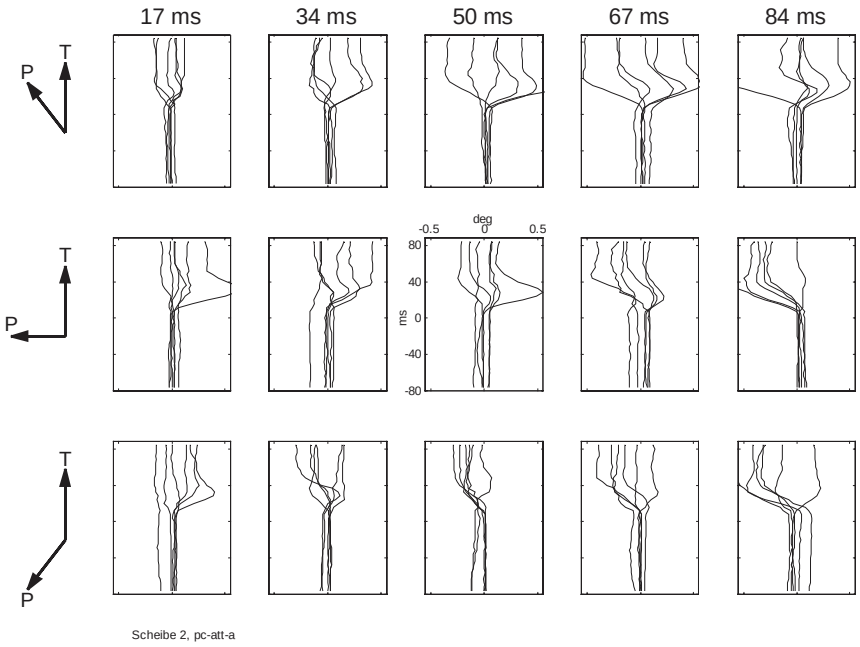


Figure 44: Average saccade locked deviation from a straight path towards the peripheral marker for each subject. If the prime was presented next to the target location, effects varied highly between subjects.

Analyzing the trajectories in conjunction with response speed showed that the high variability of gaze trajectories was due to saccades with early onsets (figure 45). Peripheral primes with high task relevance produced highly variable deviations in saccades with early onsets. Saccades with late onsets showed signs of prime inhibition, but only when the prime was presented close to the target location.

Statistical analyses. AOVA of the horizontal component of saccade lading positions produced a significant effect for SOA, congruence and the interaction SOA×congruence (SOA: $F_{4,20} = 7.724$, $p_{HF} = .023$; congruence: $F_{5,25} = 5.1$, $p_{HF} = .002$; SOA×congruence: $F_{20,100} = 5$, $p < .001$, $p_{HF} = .03$). The interaction was due to the finding that congruence conditions of 45, 90, and 135° produced deviations towards the cue whereas the congruent, neutral, and the antagonist direction (180°) did not produce any gaze deviations.

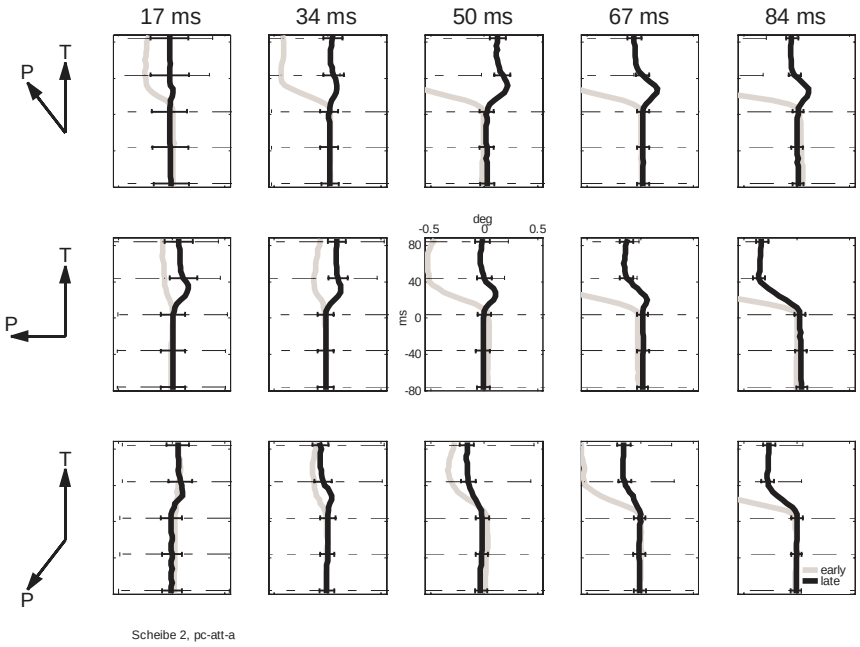


Figure 45: Saccade locked mean deviation of gaze trajectories from a straight path towards the peripheral marker and confidence intervals. Trajectories of saccades with early (gray) and late onsets (black) are shown, as well as average trajectories from figure 43. Dash-dotted error bars show confidence intervals for saccades with early onsets, solid error bars show confidence intervals for saccades with late onsets.

2.4.2.4.2 Saccade amplitude

Compared to experiment 3 (figure 34) behaviorally relevant primes had a stronger influence on saccade amplitude, which decreased with incongruent but not with congruent primes (figure 46). As in experiments 1 and 2 with central symbolic primes (figures 17 and 26), antagonistic peripheral primes (180°) produced the least gain-decrease among incongruent primes, suggesting that they suffered least from prime inhibition.

Gain of the primary saccade (fig. **46**) showed a dependency of SOA ($F_{4,20} = 13.7$, $p < .001$) as well as of congruence ($F_{7,35} = 6.7$, $p < .001$). SOA and congruence interacted significantly ($F_{28,140} = 1.7$, $p = .023$; $p_{HF} = .153$). Contrasts revealed that the significant interaction was due to gain differences between the congruent and incongruent conditions ($F_{1,5} = 15.8$, $p = .011$).

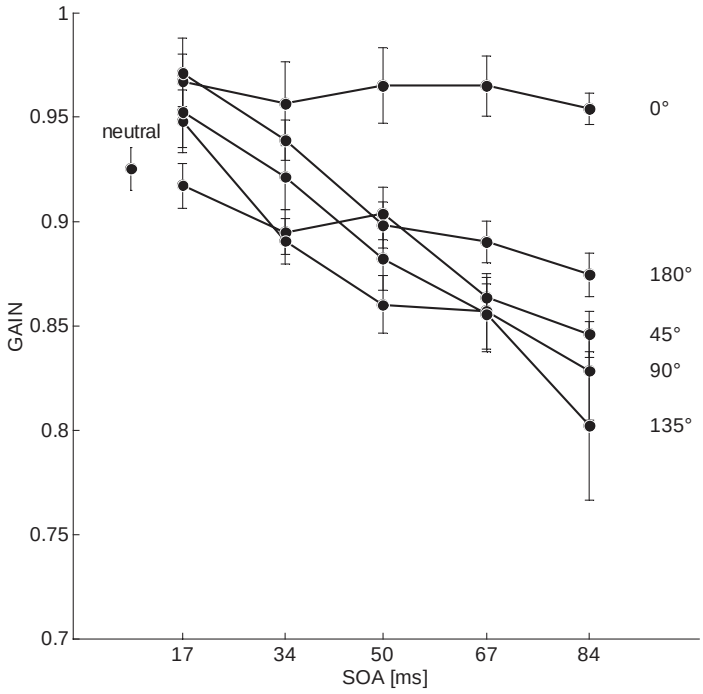


Figure 46: Gain of the primary saccade as a function of SOA and congruence

2.4.2.5 Saccade velocity

Saccade velocity profiles became dramatically lower with incongruent primes as a function of SOA (figure 47). With an SOA of 84 ms the peak of velocity profiles with congruent primes was 80°/s higher than in the slowest condition with incongruent primes (135°). Height of velocity profiles was ordered by congruence, with lower congruence leading to lower velocities. Again, the 180° condition was the exception, producing velocity profiles comparable to the 45° condition. The same pattern was reflected in saccade peak velocities (figure 48) and in gain (see figure 46 above). These results provide further evidence that primes at locations far from the target location suffer the least prime suppression among incongruent primes, leading to slower movements. Saccade duration was approximately 53 ms in all conditions.

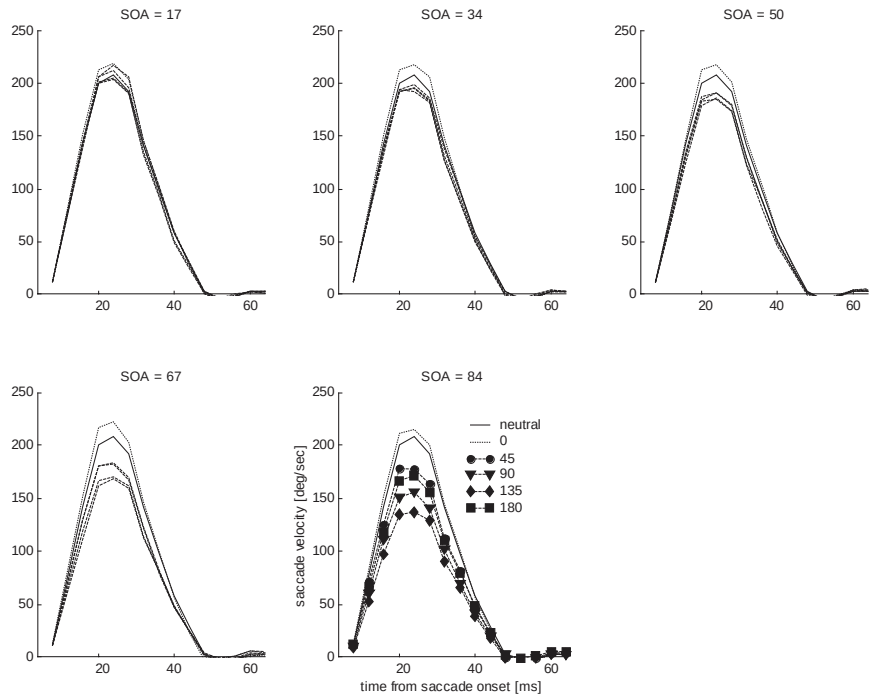


Figure 47: Velocity profiles as a function of congruence and SOA. With long SOA and incongruent primes, movements were slower than with congruent primes.

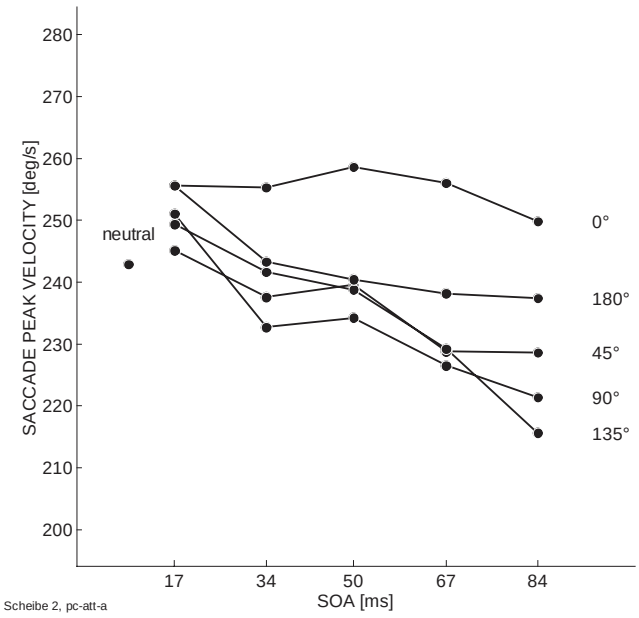


Figure 48: Mean saccade peak velocity remained constant over SOA in congruent trials, but was lower in incongruent trials.

Congruence ($F_{4,20}$ = 13.1, p < .001, p_{HF} = .001) and SOA ($F_{4,20}$ = 6.7; p = .001, p_{HF} = .035) produced significant main effects but no interaction ($F_{16,80}$ = 1.66; p = .074) in saccade peak velocity (see figure **48**). When cue and target were congruent, peak velocity was higher than in incongruent conditions ($F_{1,5}$ = 22.9; p = .005).

2.4.3 Discussion

Experiments 3 and 4 show that peripheral primes led to substantially smaller priming effects than central symbolic primes in experiments 1 and 2. Small priming effects cannot be explained with subjects having ignored the prime. Prime localization trials were presented unpredictably in experiment 4, and subjects were able to indicate were primes had been presented (figure 37). Further, primes had dramatic influence on kinetic saccade parameters. With long SOAs and incongruent primes, saccade amplitude (gain) and velocity were substantially decreased compared to congruent primes and the neutral condition, in which the target stimulus was presented alone. The results suggest that prime and target must share the critical attributes in order to produce priming effects as predicted by the accumulator model.

Increasing the behavioral relevance of primes in experiment 4, combined with peripheral priming, produced strong gaze deviations towards the primed locations. However, gaze trajectories for near primes (45°) showed signs of prime inhibition when saccade onset was late. Further evidence for prime-inhibition is provided by decreasing saccade amplitudes and velocities after incongruent priming. All these kinetic as well as reaction time effects increased with SOA. Kinetic effects all had in common that the 180° condition was less affected than the other incongruent conditions. This finding is taken as evidence that there operate inhibitory processes at the stage of motor programming which operate stronger on near than on far distractors. There was no evidence of qualitative differences of kinetic effects between central symbolic and peripheral, purely spatial primes.

2.5 General Discussion

Recent studies in masked priming have reported compelling evidence that primes influence manual reaction times to masking targets (Neumann and Klotz, 1994; Leuthold and Kopp, 1998; Vorberg et al., in prep.) using the technique of Metacontrast Dissociation (Wolff, 1989; Wolff and Klotz, 1995). Vorberg et al. showed that perception of the prime and its motor effect on the masking targets obey different temporal dynamics. Priming effects increased monotonously with SOA whether primes were invisible or whether their visibility followed a U-shaped time course (type B masking). Vorberg et al. presented a simple accumulator model, which accounted for reaction time and error data observed in masked priming. The objective of the studies presented here was to investigate whether comparable priming effects also occurred in eye movements. Congruence of primes and targets was varied parametrically in order to probe the accumulator model in situations with more than two response alternatives with different degrees of similarity. Next to reaction time measures it was possible to analyze kinetic features of eye movements, which allowed investigating whether primes only affected reaction times or whether they additionally altered motor parameters of the primed response.

Priming of eye movements produced smaller effects than predicted by the accumulator model

A consistent finding of studies about masked priming is that in metacontrast masking congruent primes lead to shorter reaction times than incongruent primes (Wolff, 1989; Neumann and Klotz, 1994; Leuthold and Kopp, 1998; Vorberg et al., in prep.). This finding was replicated in all of the four eye movement experiments. Further, the priming effect $RT_{incongruent} - RT_{congruent}$ increased linearly as a function of SOA as predicted by the accumulator model. On the other hand, priming with central symbolic primes and with peripheral spatial primes showed smaller than unit slope (figure 49). Symbolic primes with low or high validity produced slopes of .794 and .737 respectively. Peripheral spatial primes produced slopes of .207 when they were task irrelevant and of .471 when they had to be attended.

These results stand in contrast to the key prediction of the accumulator model. The simplest version of the accumulator model as presented by Vorberg et al., assumes that 1) primes and targets are processed identically, and 2) accumulators saturate. If both conditions are met, slope of priming effects is bound between 1 and 2. If only condition 1 is met, slope equals 2SOA. Therefore, with identical processing of primes and targets saturation cannot explain slopes below unit slope (see figure 6).

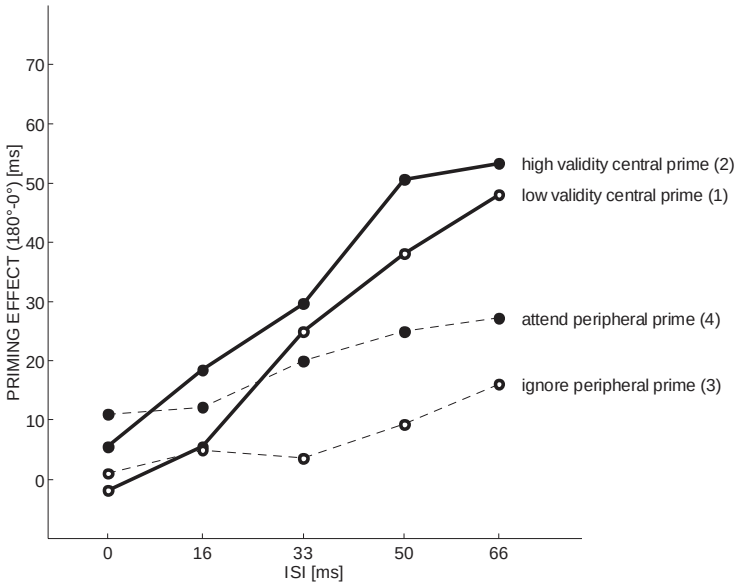


Figure 49: Priming effects ($RT_{180°}$-$RT_{0°}$) in experiments 1-4. Central symbolic primes (expts. 1, 2) produced priming functions close to unit slope (.794 and .737). Priming effects were substantially smaller when peripheral spatial primes were used which were either behaviorally irrelevant as in experiment 3 (slope = .207) or relevant as in experiment 4 (slope = .471).

Priming effects with smaller than unit slope could have resulted from processing primes with a lower rate than targets. Figures 50 and 51 compare the predictions of the accumulator model for the case that primes and targets are processed identically vs. if primes are processed with half the rate of targets.

Simulations of identical vs. different processing of primes and targets were performed with a deterministic version of the accumulator model, which predicts the central tendencies of accumulator states and priming effects (see Vorberg et al., in prep.). Accumulator state at time t is defined by

$$n(t) = \frac{\lambda + \lambda_b}{\nu}\left(1 - e^{-\nu t}\right) + n_0 e^{-\nu t}$$

with base rate $\lambda_b = 0$, saturation $\nu = .002$, each accumulator started with $n_0 = 0$. When simulating identical processing of primes and targets, processing rate rate λ was identical for primes and targets, $\lambda_{prime} = \lambda_{target} = 1$. Weaker processing of primes was simulated by driving the accumulators with $\lambda = \lambda_{prime} = 0.5$ for SOA processing cycles and with $\lambda = \lambda_{target} = 1$ for the remainder of the simulated trial. SOA was varied from 300 to 700 in steps of 50 processing cycles. Response tendency is the difference between the states of two accumulators representing left and right responses, respectively. Reaction time is defined as the time *t* at which response tendency exceeds threshold *c* (see figures 5 and 6).

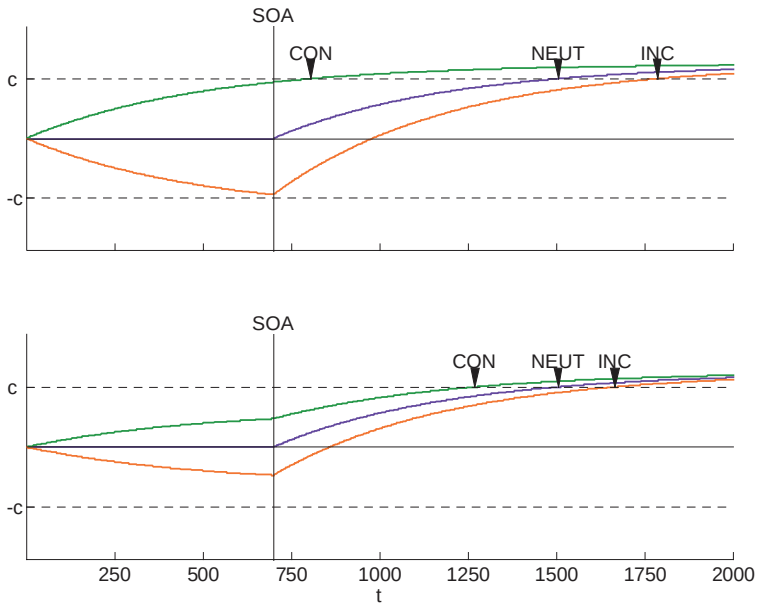


Figure 50: Time course of response tendency in the accumulator model for identical processing of primes and targets (upper panel) and for the case that primes are processed with half the rate of targets. In the former case $RT_{INC} - RT_{CON} \approx SOA$. Only SOA = 700 shown here. If primes are processed at lower rates than targets, priming effects with slope smaller than one can occur (here 0.4). Reactions are initiated when response tendency exceeds threshold *c*.

Peripheral primes in experiments 3 and 4 may have been processed with lower rates than centrally presented symbolic target stimuli because:

1) Primes and targets were not at the same location. But this does not seem per se a critical factor. Vorberg (unpublished data) has shown that the priming effect remains in the same order irrespective of whether primes and targets are presented at the same or at different locations.

2) Peripheral primes could have been ignored. This interpretation can be excluded in experiment 4, in which primes were task relevant in one third of the trials, and subjects were able to report prime location. But still, their relative large distance to the imperative stimulus (5° visual angle) may have reduced their influence in priming.

3) Peripheral primes did not share all critical attributes of the target stimulus. Although peripheral primes induce congruence by indicating a direction for the saccade, primes may have a stronger influence if they share geometrical features with the target. If target color determines the reaction, prime color should produce the strongest priming effects (see Schmidt, 1997). Possibly, if primes lack critical features of targets, their processing may have weaker links to the accumulators driven by the targets.

On the other hand, there is no convincing reason to assume different processing rates for central symbolic primes compared to central symbolic targets in experiments 1 and 2, even if primes were half the size of targets, but this was also true in the experiments of Vorberg et al., and did not lead to reduced slopes there. Further, symbolic primes shared all critical shape attributes of targets. Yet, lower processing rates of primes cannot be excluded, although response selection mechanisms provide an alternative account (see below).

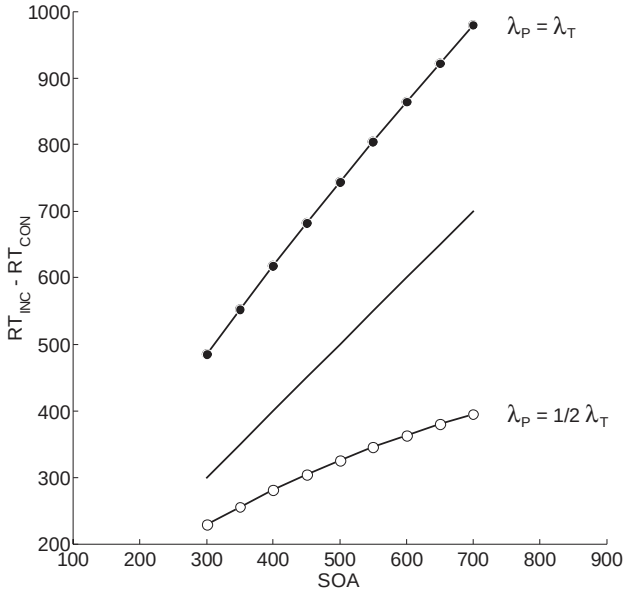


Figure 51: Predicted priming effects if processing rate of primes (open markers) is half the size of the processing rate of targets (filled markers). The diagonal indicates unit slope. The priming effect for $\lambda_P = \lambda_T$ had a slope of 1.2, the priming effect of $\lambda_P = \frac{1}{2}\lambda_T$ was 0.4. Priming functions are only linear if primes and targets are processed identically.

Priming effects varied as a function of prime-target congruence

Parametrical variation of congruence revealed that small differences between prime and target orientation resulted in shorter saccadic reaction times than large differences. This indicates that priming is not a categorical process but that it can rely on analogue representations in which processing is based on similarity. The data are consistent with neurophysiological data, for example of orientation- or direction-selective processing in striate and extrastriate cortex (Maunsell and Van Essen, 1983). Stimuli with similar critical attributes drive similar populations of neurons. Priming could be related to the interaction of activity in neural populations, generated by primes and targets.

When activity exceeds threshold in populations that code a particular attribute, further processes may be triggered, for example initiating a movement. Incongruent primes and targets might either activate separate neural populations which interfere if both project to the same structure or they interfere on the level of tuned neurons, which are, for example excited by the prime but inhibited by the target. These assumptions will be the basis to extend the accumulator model in the simulation chapter. Different response alternatives are represented in populations of orientation- or direction-sensitive accumulators whose processing mechanisms take into account similarity of the current input with the accumulators' preferred stimuli.

The order of reaction time functions by congruence was violated by the 180° condition, which produced shorter reaction times than the 135° condition in experiments 1 to 3 (figures 13, 23, and 30), but not in experiment 4 (figure 40). It was suggested, that primes pointing far away from the target direction were treated differently from other incongruent primes pointing closer to the target. This suggestion was further analyzed in the kinetic parameters of eye movements.

Primes had access to motor programming

Masked primes did not only influence saccadic reaction times but also systematically affected direction of gaze, its velocity and its amplitude. The perhaps most striking finding was the direction of gaze deviations. It was expected that if primes had access to response preparation at the level of motor preparation, that gaze might deviate towards the direction indicated by the prime. Surprisingly, the contrary happened in experiments 1 and 3 if primes were pointing next to the target position (45°), or if prime and target direction were perpendicular (90°). See figure 52 for an overview.

Response speed predicted the direction of gaze deviations

Gaze deviations contralateral to prime orientation were interpreted as evidence for suppression of prime- related response preparation. The underlying idea is that primes and targets both generated motor programs for saccades in their corresponding conditions. Compromise ocular responses, with saccades landing at intermediate positions, have been observed in double-stimulus experiments, in which two imperative stimuli (Becker and Jürgens, 1979; Aslin and Shea, 1987; Findlay, 1997) or a target and a distractor (Theeuwes et al., 1998) are presented simultaneously. In the experiments presented here, primes and targets were presented with varying SOA. This may result in an asynchronous buildup of motor programs, and possibly triggers response selection by which one program becomes suppressed. Temporal separation between stimuli which produce conflicting motor programs have been reported to produce gaze deviations opposite to the 'deselected' program instead of a compromise response (Sheliga et al., 1994, 1995).

The data contained in figure 52 provides further insight into the underlying dynamics of deviation effects. Gaze deviations towards or away from the prime seemed to reflect the relative timing between the onset of suppression with respect to movement initiation. With short asynchrony, incongruent primes had less time to generate a program that could conflict with the program related to the target. This is consistent with the data, which revealed only minor gaze deviations with short SOAs. Response speed, however, determined whether the saccade started early or late with respect to suppression. If saccades started early, they were partly controlled by residual prime related activation. If saccade started late, prime related activation had been suppressed below baseline, leading to gaze deviations contralateral to the program that was generated by the prime.

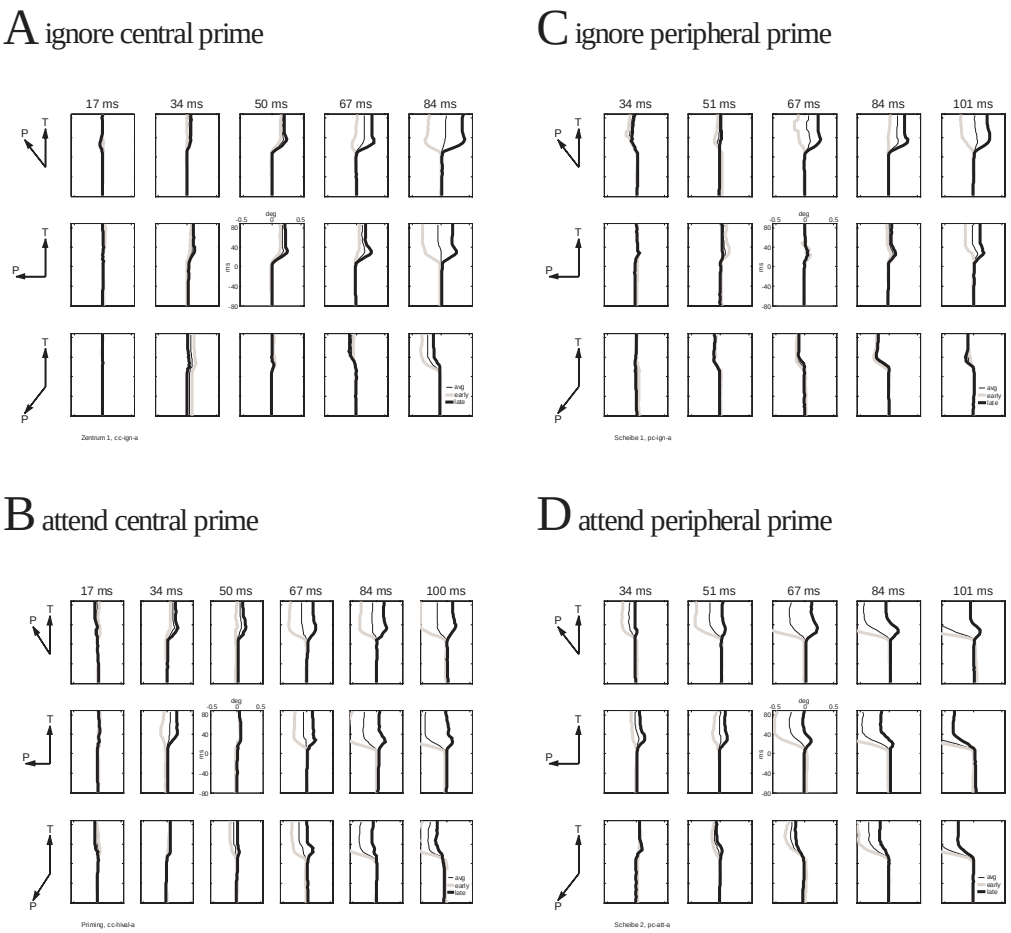


Figure 52: Median split of saccadic reaction time for each subject under each condition revealed deviations towards prime direction in early saccades and away from primes in late saccades if incongruence of primes and targets was small (45°) or intermediate (90°). With 135° congruence, gaze direction always deviated in direction of primes, although less prominent in saccades with late onsets.

Other parameters of saccade metrics were influenced by primes, as well. Saccade amplitude and velocity decreased with incongruent primes as a function of SOA in all four experiments reported here. Antagonist primes did neither produce the longest reaction times, nor the lowest amplitudes, nor the slowest saccades. All these measures indicate that, if suppression of prime related activation exists, it affects those primes stronger, which point closer to the target location than those primes that point far away.

2.5.1 What is primed in masked priming?

The analysis of eye movements in four masked priming experiments has revealed that primes influence the decision when a movement is initiated, and that primes take part in response preparation at the motor level. The results render it unlikely that decision and response preparation processes were strictly serial, in a sense that response preparation did not start before the imperative stimulus had been fully processed. If this had been true, then an incongruent prime would have either produced an error, or a delay. The target should have exclusively controlled movement parameters, then. The data showed that incongruent primes delayed decisions and affected motor parameters as saccade direction, amplitude and velocity.

2.5.1.1 Motor areas...

Recent evidence from event related potential (ERP) studies and from functional brain imaging indicates that masked primes, even those that escape awareness, generate covert motor activity in manual reaction tasks. Leuthold and Kopp (1998) employed a spatially modified version of the metacontrast masking experiment by Neumann and Klotz (1994) shown in figure 2. Using lateralized readiness potentials, which allow computing activation of specific motor responses from ERPs (Coles et al., 1988), Leuthold and Kopp (1998) showed that incongruent primes produced an initial activity for the incorrect hand before the correct response was given. A comparable result, initial LRP activation of the correct hand after congruent primes, and of the incorrect hand after incongruent primes, was reported by Dehaene et al. (1998). Moreover, the authors showed with event related functional magnetic resonance imaging, that the effect of covert prime activation observed in LRPs was located in the motor cortex. The results of both studies clearly indicate that masked primes not only influence decision processes but also activate motor areas of their corresponding response. Thus, incongruent masked primes are likely to generate interference with the target in decision as well as in motor selection processes.

2.5.1.2 ... but not the perceptual system?

Macknick and Livingstone (1998) compared the temporal characteristics of visual masking in humans with the corresponding neuronal responses in the primary visual cortex of monkeys. They showed that in backward masking, the onset of the target stimulus suppressed the prime's transient off-response, a signal that usually occurred approximately 200 ms after prime offset. The time course of suppression of the transient off-response paralleled the typical time course of backward masking (type-B masking, Breitmeyer, 1984). The data suggest that neuronal responses in early visual areas may be important for stimulus visibility.

2.5.1.3 Perception and action

This does not mean that prime information gets lost early in visual processing, though. Primary visual areas do not exclusively reflect early visual processing. They are also driven by feedback processes of higher visual areas (Edelman and Mountcastle, 1978; Felleman and Van Essen, 1991; see discussion in Young, 1995). Priming effects are proof for successful semantic processing of the prime in masked priming tasks. The semantics are not trivial: Shapes as arrows or diamonds and squares, even digits and number words (Vorberg, unpublished data; Dehaene et al., 1998) can be successfully linked to the corresponding response without reaching awareness. It is possible, though, that suppression of critical information in primary visual areas destroys subjects' awareness of the prime (Bridgeman, 1980, 1988) after sufficient information for stimulus response coupling has been collected.

Dissociations of priming and awareness are in line with concepts of a functional separation of visual processing into a stream devoted to object recognition and a stream for motor control (Milner and Goodale, 1995). But the dissociations observed in masked priming do not necessarily originate from these streams (see Neumann et al., 1998). Processing stimulus identity and linking it to corresponding motor behavior may be the outcome of processing in different pathways, which separate early in the hierarchy of visual processing. But identification and response generation may be processed within the same stream as well, and separate thereafter. While one branch is engaged in motor control, the other one is engaged in evaluation purposes, for example in collecting evidence from primary visual areas, to check if there actually was a visual stimulus which has triggered the current behavior or if it was a false alarm.

Thus, whether processing of perceptual and action related aspects takes place in different streams or not, will not be of importance for the model of priming presented here. It will be assumed that congruence effects rely on a structure in which identities of primes and targets are linked to their corresponding motor behaviors. Reaction time patterns suggest, that processing in such a structure is based upon similarity between stimulus-response couplings of primes and targets. The following chapter presents an attempt to simulate such a structure and thereby to account for effects of primes on reaction time as well as on motor parameters.

Chapter 4

A neural network model for priming of eye movements by masked stimuli

The effect of a prime on reactions triggered by a target stimulus have been shown to depend on the degree of congruence between prime and target and on their SOA. The more time can be spent on processing the prime the stronger is its effect. The accumulator model by Vorberg et al. was defined for two responses, left vs. right. To account for the findings reported in experiments 1 to 4 an extension of the model is needed so that it can represent stimuli and responses of different orientations and directions in two-dimensional space. Figure 53 shows the general architecture of the model. An input representing an oriented stimulus, for example an arrow, is fed into a sensory store. From there, activation propagates gradually to accumulators, which have a defined sensitivity for particular stimulus orientations. Each accumulator represents a tendency to respond with a movement in a particular direction. The sum of all accumulators represents an overall response tendency with a defined direction and strength. If strength exceeds threshold, a response in direction of the response tendency is generated.

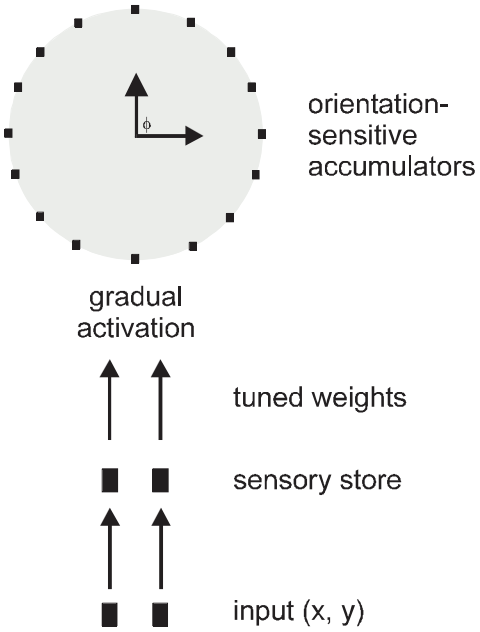


Figure 53: Directional input feeds into a sensory store, which gradually activates orientation-sensitive accumulators, each representing the tendency for a movement in a particular direction. Each accumulator contributes a directed response tendency weighted by its activation level leading to an overall response tendency with a particular direction and strength.

3.1 Representation of quantities

The following terms will be used to describe the model. A *response* refers to an overt movement from the center of fixation to a saccade target, *response tendency* is a measure for the trend to perform a particular response, and *input* stands for a stimulus, which indicates a particular response. A *vector* is a mathematical means to represent directed quantities, for example movement, force, and velocity. The model will employ vectors to describe responses, response tendencies, and input stimuli. A two-dimensional vector **v** with direction ϕ and length l is equivalently defined by its components **v** = (x, y) (see figure 54). The components x and y can be computed from ϕ and l as:

$$\mathbf{v} = l(\cos \phi, \sin \phi) \qquad \text{(eq. 1)}$$

In the accumulator model by Vorberg et al., two accumulators represented antagonistic response tendencies. Accumulators were connected to response units, which triggered the appropriate response, when the difference between the accumulator states exceeded threshold. Multiple response directions will be embodied in the current model.

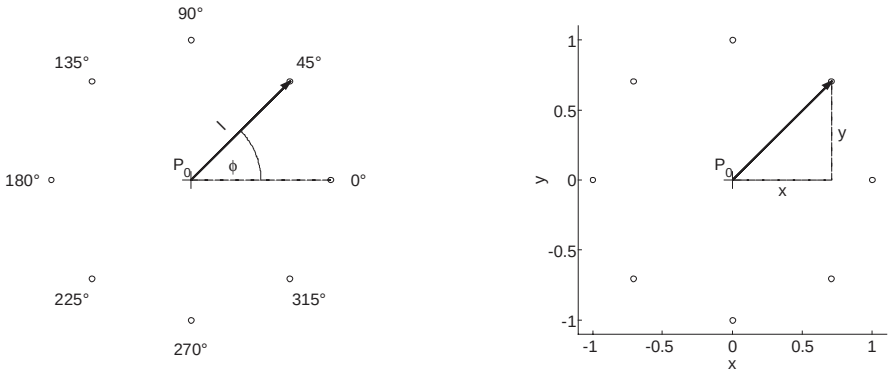


Figure 54: **A**, Representation of a vector **v** by its direction ϕ and its length l. **B**, Representation of the same vector by its x- and y-components $\mathbf{v} = l(\cos\ \phi, \sin \phi)$.

In the experiments presented in chapter two, a response was an eye movement, which is represented here by a vector **r** with a particular direction ϕ_r and a particular length l_r, written as $\mathbf{r} = l_r(\cos\ \phi_r, \sin\ \phi_r)$. Accumulators, which represent response tendencies, are viewed as pulling forces aligned with a particular response, with $\mathbf{a} = l_a(\cos\ \phi_a, \sin\ \phi_a)$. An input stimulus is a vector with unit length, ad regarded as a placeholder for a response in a particular direction.

3.2 Processing of information

Processing of information in the model is based on processing of similarities between vectors. Stimuli drive those accumulators most that create a response tendency, which is aligned with the orientation of the stimuli. Accumulators drive those response units most that generate a movement in the accumulators' preferred direction. An accumulator **a** and its preferred response **r** have the same direction ($\phi_a = \phi_r$).

The similarity between two vectors **p** and **q** is a function of the size of the angle between them (ϕ_p - ϕ_q), if both have unit length:

$$\mathbf{p} \bullet \mathbf{q} = |\mathbf{p}| * |\mathbf{q}| * \cos(\phi_p - \phi_q) \qquad \text{(eq. 2)}$$

with |**p**| = length of **p**, and |**q**| = length of **q**.

Assume that **p** and **q** have unit length (|**p**| = |**q**| = 1), then

$$\mathbf{p} \bullet \mathbf{q} = \cos(\phi_p - \phi_q) \qquad \text{(eq. 3)}$$

Similarity ranges from –1 for complementary vectors to +1 for identical vectors.

3.2.1 Processing of input

In the accumulator model, input was processed with two accumulators with a fixed rate of λ to which the base rate λ_b was added. In the extended model, several accumulators representing different preferred movement directions will be employed. The rate λ_a, by which an accumulator is driven, is a function of the similarity of the input vector **i** with the accumulator's preferred response **r** plus a constant base rate λ_b. With unit length of input vector and response vector:

$$\lambda_a = \cos(\phi_i - \phi_a) + \lambda_b \qquad \text{(eq. 4)}$$

Each accumulator is driven by each stimulus.

3.2.2 Activation function

An accumulator is driven with a netto input rate $net = \lambda_a + \lambda_b$. The rate is transformed to an activation state of an accumulator by means of a logistic activation function:

$$f(net) = \frac{1}{1+e^{-net}} \qquad \text{(eq. 5)}$$

This function is chosen because it scales input to output values between 0 and 1. Negative input leads to positive output below baseline, positive input to positive output above baseline (figure 55).

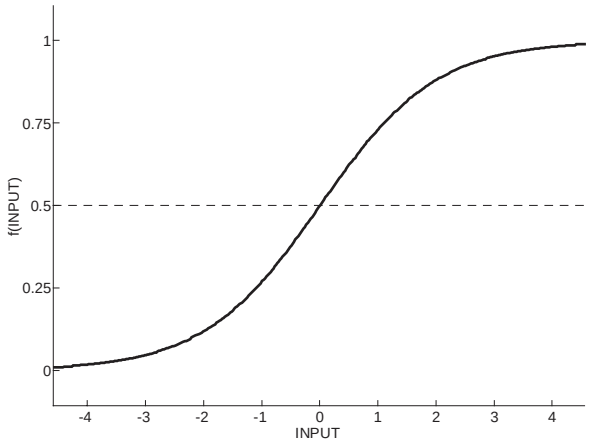


Figure 55: Sigmoid activation function. Negative input leads to output values below, positive input to output above baseline, with f(0) = 0.5. Output is bound between 0 and 1.

3.2.3 Tuning functions

Neurons in the motor cortex as well as in visual areas have been shown to be sensitive to motion direction and stimulus orientation with cosine tuning functions as in eq. 4 (Georgopoulos et al., 1982; Maunsell and Van Essen, 1983). Cell activity was highest for a movement in a particular direction and decreased progressively with movement directions farther away from this direction. A simulated tuning function for a neuron which is maximally sensitive to a leftwards oriented input stimulus ($\phi_a = 180°$) is shown in figure 56.

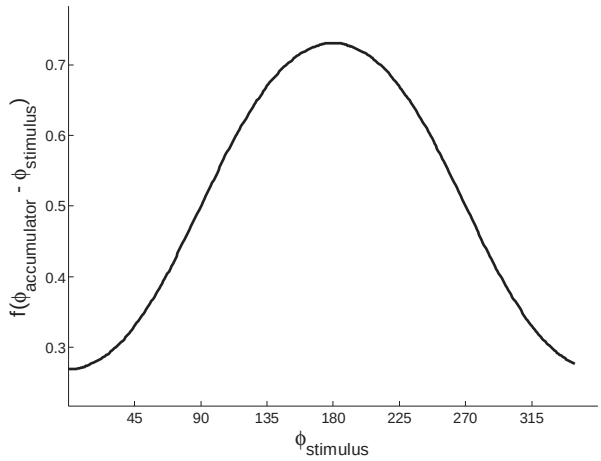


Figure 56: Tuning function of a hypothetical accumulator that is maximally sensitive to a leftwards-oriented input stimulus ($\phi_a = 180°$). Input rate decreases when the angle between stimulus orientation and the accumulator's preferred direction increases.

3.2.4 Dynamics of activation

Two factors determine the temporal dynamics of the model: 1) Activation strength of accumulators l_a changes gradually, and 2) accumulators saturate through decay processes. The activation strength *la* of accumulator *i* at time *t* is defined through:

$$la_i(t) = (1-\tau)la_i(t-1) + \tau f(net_i(t)) \qquad \text{(eq. 6)}$$

with $0 < \tau \leq 1$

The parameter τ determines the speed of gradual changes as well as strength of decay. Small values of τ induce little decay and small changes from time step to time step (figure 57). τ was .05 throughout all simulations.

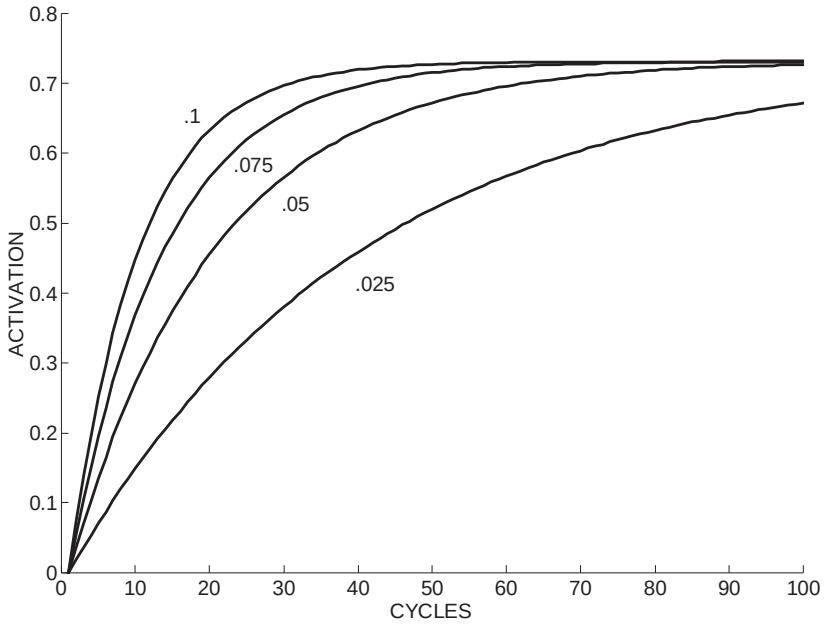


Figure 57: Time course of gradual activation function for four different levels of τ. Input is 1, bias is -1 (i.e. a net input of 0). Speed of convergence depends on the parameter τ, with higher values leading to faster convergence.

Figure 59 shows the time course of activation for 32 accumulators when a stimulus pointing to the left (ϕ =180°) was applied to the model. Activation of accumulators developed gradually. All accumulators started at baseline, those accumulators which had preferred directions close to stimulus orientation were activated strongest, accumulators tuned to the opposite direction (ϕ_a = 0°, at the very left of the figure), were driven below their baseline activation.

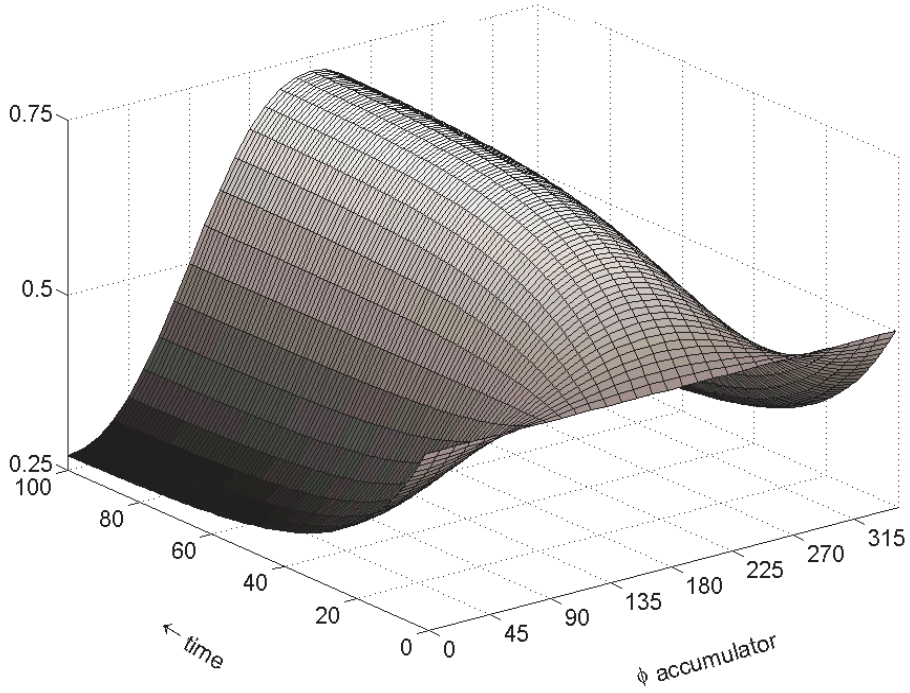


Figure 58: Gradual activation in time and over orientation of 32 accumulators with preferred response directions between 0 and 347.5°. Stimulus orientation $\phi = 180°$ and $\tau = .05$. Activation of all accumulators started at baseline. Those accumulators representing response directions between 90 and 270° are excited; the others are inhibited.

3.2.5 Output state

The output of the model is the summed activity of all accumulators. The sum of vectors is itself a vector, representing the overall response tendency:

$$\mathbf{o} = \sum_{i=1}^{n} \mathbf{a}_i \tag{7}$$

The entire population of accumulators determines the response of the model. Each accumulator contributes to the response by pulling in its preferred direction according to its activation strength.

3.2.6 Population coding

When a stimulus is applied to the model, it will not activate a single optimally tuned accumulator but a whole population of broadly tuned accumulators. Response strength of each accumulator reflects the similarity between the input stimulus and the accumulator's preferred stimulus. The summed activity **o** of the entire population of accumulators represents the system's overall response tendency (eq. 7). This principle is known as *population coding*, and the sum vector is termed *population vector*.

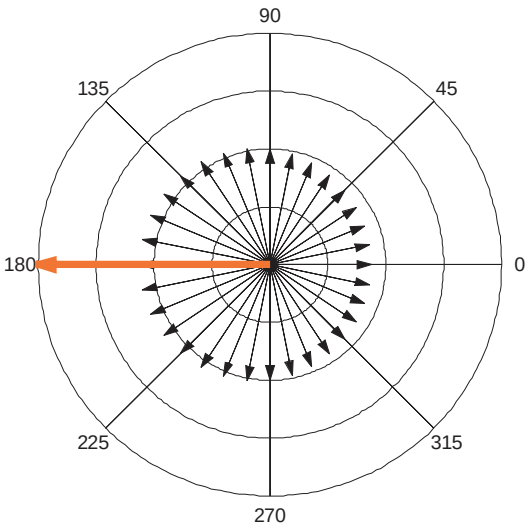


Figure 59: A stimulus pointing to the left **i** = (-.25, 0), influences the activation of the entire set of accumulators due to their broad tuning functions. Each arrow depicts the preferred direction (arrow orientation) and activation strength (arrow length) of one out of 32 accumulators. Response tendency is represented by the sumvector of all accumulators (thick arrow). Circles mark activation strengths from .25 to 1 in steps of .25. Activation strength is highest for the accumulator that has a preferred direction of 180° and decreases with angular difference between stimulus orientation and an accumulator's preferred direction. Accumulators which have their preferred directions towards the left hemifield are activated above, the others (except for 90 and 180°) below baseline (0.5).

With four orthogonally tuned accumulators, population coding can represent any response tendency. Adding further accumulators simply increases the population's robustness. Such a coding system allows that its building blocks, for example neurons, may operate with a relative low reliability. Failing to burst from time to time or even terminally due to cell damage has only little influence on the populations overall behavior, as long as these effects occur randomly throughout the population.

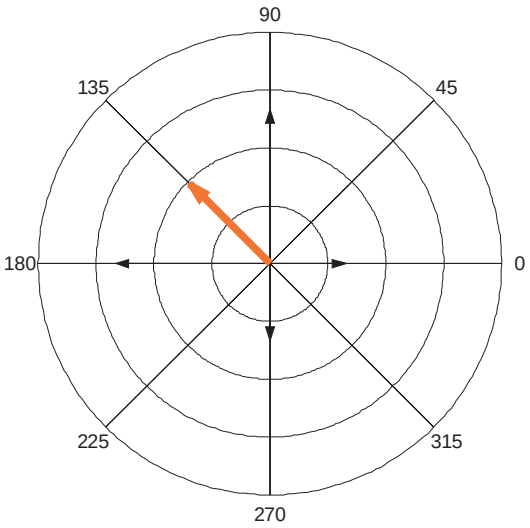


Figure : With population coding, four orthogonally tuned accumulators can represent any reponse tendency. Black arrows indicate activation of accumulators with preferred directions of 0, 90, 180, and 270°. The input stimulus had an orientation of 135°, **i** = (-.7, .7). The population vector has direction of 135°, although no accumulator had 135° as its preferred direction.

Neurophysiological data from direction-sensitive cells in the motor cortex of monkeys was analyzed by assigning each neuron a vector that represented the neuron's preferred movement direction (vector orientation) and its current spike rate (vector length). Georgopoulos and colleagues showed that the direction of arm movements in two-dimensional space was predicted with high reliability by the summed vector of neural activity, that is by the population vector (Georgopoulos et al., 1983, 1986, 1988).

There is a large body of evidence that representation of stimulus attributes (Maunsell and Van Essen, 1983;), spatial information (Steinmetz et al., 1987), and movement direction of limbs (Kalaska et al., 1983) and eyes (Lee et al., 1988) are population coded. Response tendency in the extended accumulator model is population-coded, as it represents the summed activity of directionally tuned accumulators. Population coding has been successfully applied to analyze movement direction and force (Georgopoulos et al., 1983, 1992). The following simulations will show whether a population-vector model can predict priming effects for primes and targets of varying congruence and SOA.

The fundamental assumption is that reaction time is determined by the time when the length of the population vector (|**o**|) exceeds threshold. If prime and target are congruent, they drive the same accumulators and the summed activity reaches threshold fast. If primes and targets are maximally incongruent, they drive different sets of accumulators that cancel each other out when summed up. Therefore threshold is reached later, after prime-related activity has decayed. Congruence effects are expected because similar stimuli drive similar accumulators. SOA effects are expected because processing is gradual. The model will be compared to the experimental data and to the predictions of the accumulator model of Vorberg et al.

3.3 Simulations

Simulations were implemented and performed with MATLAB. The model contained 32 accumulators. In principle, four accumulators would have been sufficient to represent all movement directions, but in the second part of the simulation a higher number of accumulators was required in order to implement a spatial filter.

3.3.1 Stimuli

Input vectors were two-component (x and y) vectors of unit length and different directions. Prime direction varied from 0° to 180° in steps of 45° leading to input vectors: $\mathbf{i}_{\mathbf{prime\_0}}$ = [1, 0], $\mathbf{i}_{\mathbf{prime\_45}}$ = [.707, 0], $\mathbf{i}_{\mathbf{prime\_90}}$ = [0, 1], $\mathbf{i}_{\mathbf{prime\_135}}$ = [-.707, 0], and $\mathbf{i}_{\mathbf{prime\_180}}$ = [-1, 0]. For neutral trials $\mathbf{i}_{\mathbf{prime\_neutral}}$ = [0, 0]. The target always pointed leftwards (i.e. 180°), $\mathbf{i}_{\mathbf{target}}$ = [-1, 0]. τ was 0.05.

3.3.2 Task

The task was a simulated priming experiment using central primes with different degrees of congruence. A simulated trial began with the presentation of $\mathbf{i}_{\mathbf{prime}}$ for t_{prime} = 4 cycles. The same vector was applied during the inter stimulus interval, following the assumption that primes remained in the sensory buffer during that period. After the inter stimulus interval the target ($\mathbf{i}_{\mathbf{target}}$) which was shown for the remainder of the trial. In the simulations each trial consisted of 100 processing cycles. Simulated reaction time was determined with respect to target onset as the processing cycle in which the length of the population vector (|**o**|) exceeded a threshold of 85% of its maximal length.

3.3.3 Design

SOA was varied in steps of 4, 8, 12, 20, 24, and 28 processing cycles. Congruence was neutral, 0, 45, 90, 135, or 180°. Dependent variables were reaction time and time courses of each accumulator's activation. Under each condition only one trial was run, because the model is deterministic.

3.4 Results

Figure 60 shows the time course of activation for 32 accumulators in a simulated incongruent trial (compare with a congruent trial in figure 59). Prime direction was 0° and SOA = 24 cycles. For the first 24 cycles the population of accumulators reflects prime-related activation, which breaks down at target onset.

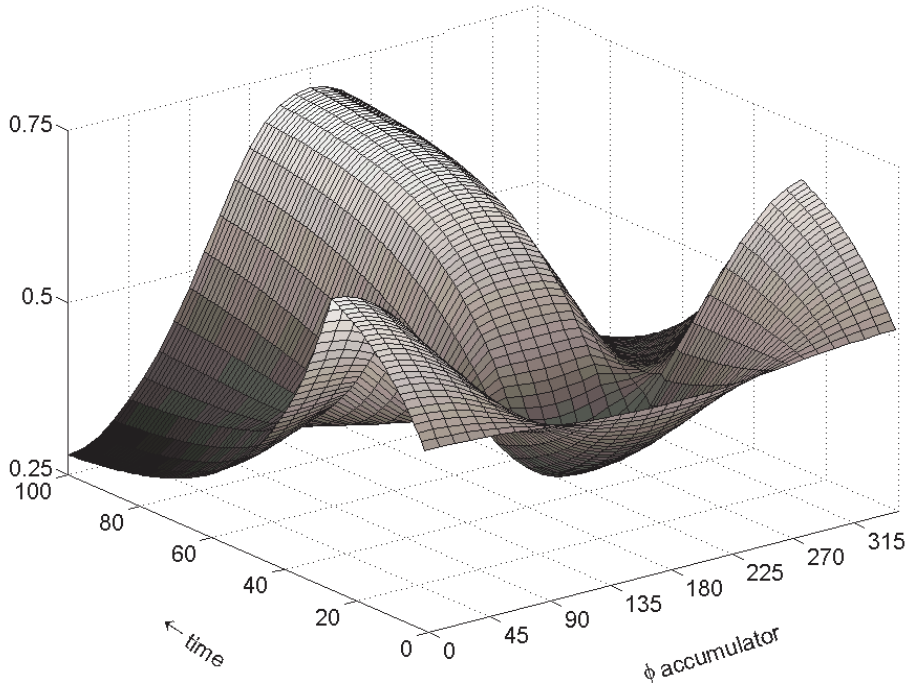


Figure 60: Time course of activation of 32 accumulators with incongruent priming. ϕ_{target} = 180°, ϕ_{prime} = 0°, congruence = 180° ($|\phi_{target} - \phi_{prime}|$), SOA = 24 cycles.

Figure **61** shows the development of the population vector length ($|\mathbf{o}|$) under the simulated experimental conditions. The time course of $|\mathbf{o}|$ shows a clearly different pattern for different levels of congruence. These differences are augmented by SOA. At the beginning of a trial all accumulators have baseline activity. They pull the overall response tendency **o** in different directions with equal force and therefore neutralize each other. Consequently $|\mathbf{o}| = 0$. During prime presentation and the interstimulus interval **o** is same for all conditions, except for neutral primes, as primes produce the same response strength irrespective of their direction. In the neutral condition a zero vector (0, 0) is presented, and all accumulators rest at baseline level until target onset.

Population vector length starts to differ between conditions, when the target is presented. If prime and target are congruent (0° condition) the population is just driven further in the same direction. In incongruent conditions, units which were previously active lose activity according to the degree of incongruence between their preferred orientation and the target. At the same time units, which are better tuned to the target, become more active.

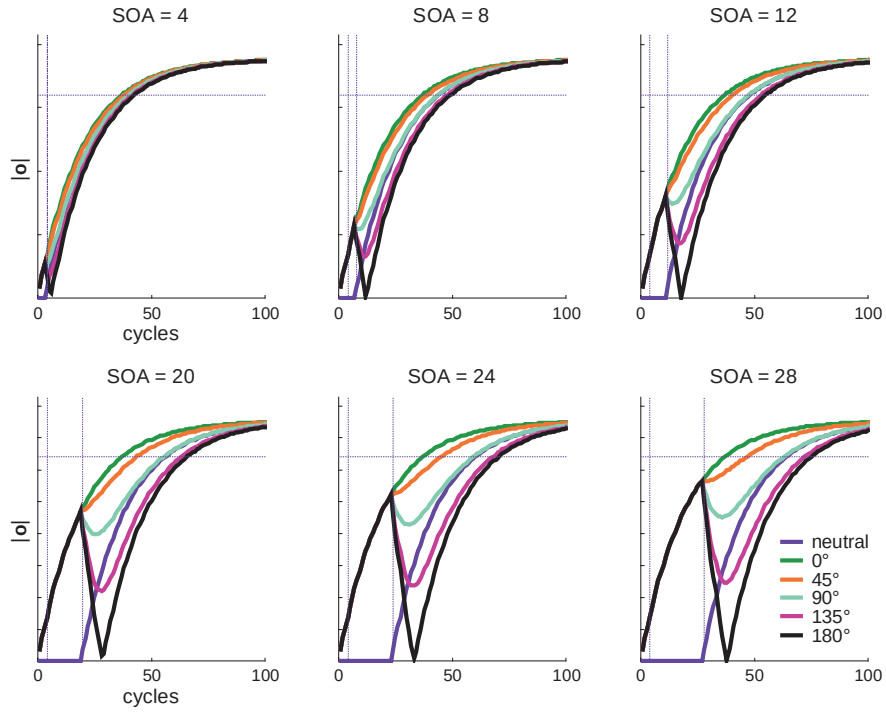


Figure 61: Each panel depicts the length of the population vector (|**o**|) as a function of time under six different simulated congruence conditions and a specific SOA. The end of prime presentation (4 cycles) is indicated by the first, the end of the interstimulus interval by the second vertical line. The target is presented for the remainder of each simulated trial. Model reaction time is the processing cycle in which |**o**| exceeds threshold (horizontal line). Threshold was fixed at 80% of the maximal length of the population vector.

With incongruent primes, the population vector length decreases during the period of activation shift from prime-related activation to target related activation for the following reason: Decay in accumulators driven by the prime is stronger than increase of activation in accumulators driven by the target. The length of the population vector does not increase until target related activity exceeds prime-related activity in the population.

3.4.1 Reaction times

Reaction times are determined when |**o**| reaches threshold. Threshold was fixed at 85 per cent of the maximal length of the population vector. Figure 62 shows the predicted reaction times of the simulated experimental conditions. The neutral condition serves as a baseline. For congruencies below 90°, reaction times become shorter as the time available for processing the prime increases. Reaction times increase for congruencies above 90°, whereas the 90° condition does not differ from the neutral condition. The model correctly predicts the order of the priming effects observed in experiments 1 to 4 with the exception that in the model but not in the data, the 180° condition produces the longest reaction times.

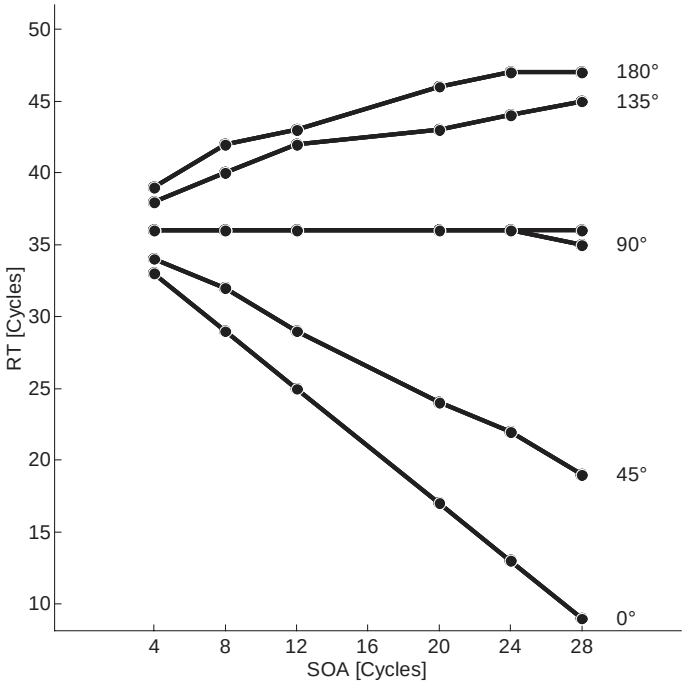


Figure 62: Predicted reaction times for different consistency conditions as a function of SOA. Reaction time functions are ordered by congruence.

The accumulator model of Vorberg et al. predicts that the slope of the priming effect $RT_{incongruent}$ - $RT_{congruent}$ is bound between 1 and 2. Figure 63 shows the priming effect $RT_{180°}$ - $RT_{0°}$ as a function of SOA. The predicted priming effect of the population-vector model increased linearly with SOA and was fitted by the function:

$RT_{180°} - RT_{0°} = 1.3\ SOA + 1.3$ cycles.

Replications with different thresholds (80, 85, 90 %) resulted in the same slope. The population-vector model predicts priming effects which are in line with the accumulator model. However, the slopes of priming effects observed in experiments 1 and 2 were below the predictions of both models and seek explanation.

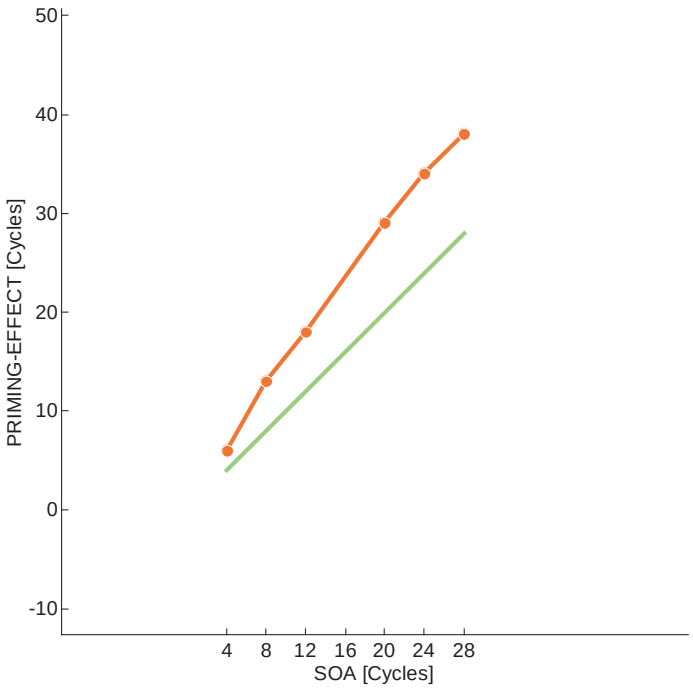


Figure 63: Predicted reaction times for maximally congruent (0°) trials were subtracted from maximally incongruent trials (180°). The priming effect (filled circles) increases linearly with SOA. The diagonal shows a theoretical priming effect with unit slope where the priming effect equals SOA.

3.4.2 Movement deviations

Georgopoulos et al. (1988) have shown that the population vector of neurons in the motor cortex predicts the direction of the upcoming movement. They visualized the movement-locked gradual development of direction and force by plotting a series of population vectors at discrete time steps. Figure 64 shows such a plot for different congruence conditions from the simulated priming experiment. A trial starts at the bottom of each panel with the presentation of the prime. The population vector **o** is shown for each time step. The target always pointed leftwards and was presented with a SOA of 28. Movement onset was the processing cycle at which |**o**| crossed threshold.

Reaction times increased with degree of incongruence. With incongruent primes the direction of population vector gradually changes, rotating from prime to target direction. In the 45° and the 135° conditions, the prime was pointing towards the upper left and the upper right respectively. The small upward component at movement onset in both conditions indicates that at this time there still exists residual prime-related activity in the population. This would predict movement deviations toward prime orientation.

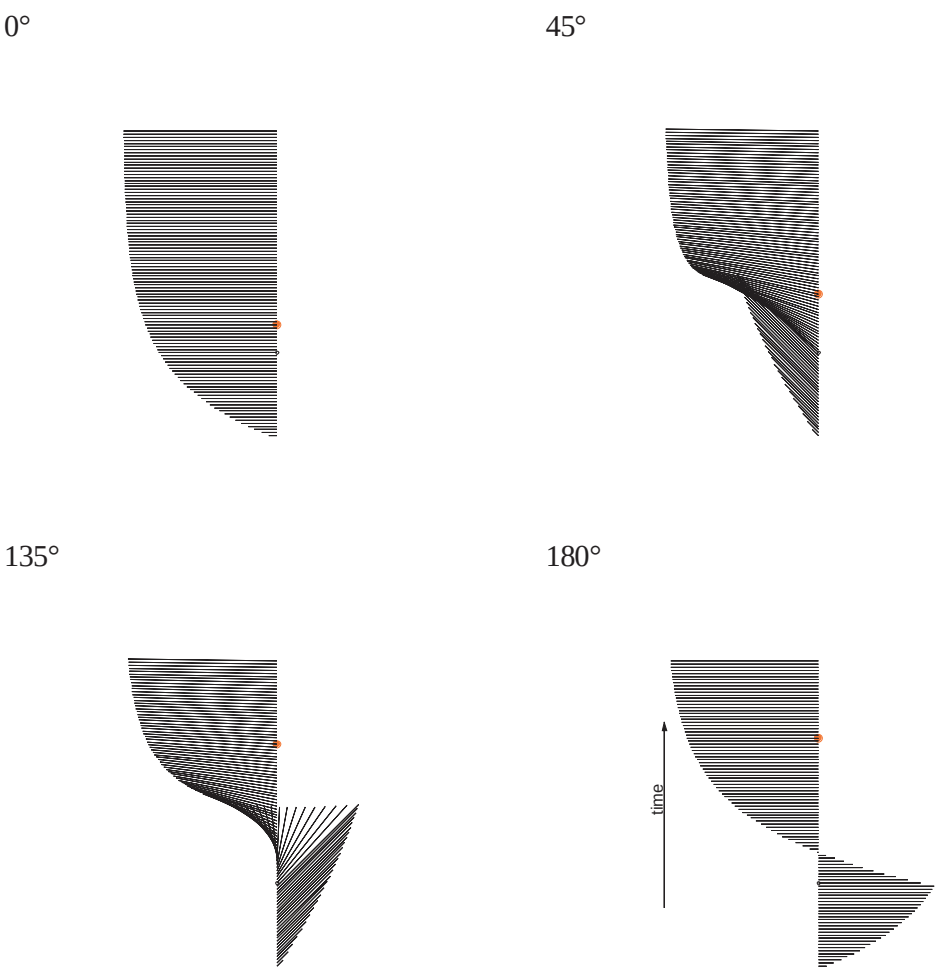


Figure 64: Time course of the population vector under four congruence levels. Each line depicts the population vector at a particular time step. The population vector builds up gradually in prime direction. After a constant SOA of 28 cycles the target was presented, always pointing leftwards (open circle). With congruent primes (0°) the population vector reached critical length first (filled marker). Reaction time is the distance between the marker for target onset and the marker for movement onset. With incongruent primes not only reaction time increased, but also the direction of population vector gradually changed, rotating from prime to target direction. In the 45° and the 135° conditions, the small upward component at movement onset indicates that at this time there still existed residual prime-related activity, which would predict movement deviations toward prime orientation.

Consequently, the model predicts movement deviations directed towards the orientation of the prime. At no time, the population contains a downward component, which would indicate a deviation of the movement trajectory away from the prime. The gaze deviations away from prime orientation, which were observed in experiments 1, 3, and 4 cannot be explained by the model. Figures 64 and 65 illustrate the time courses of activation in accumulators and the time courses of their resulting population vectors.

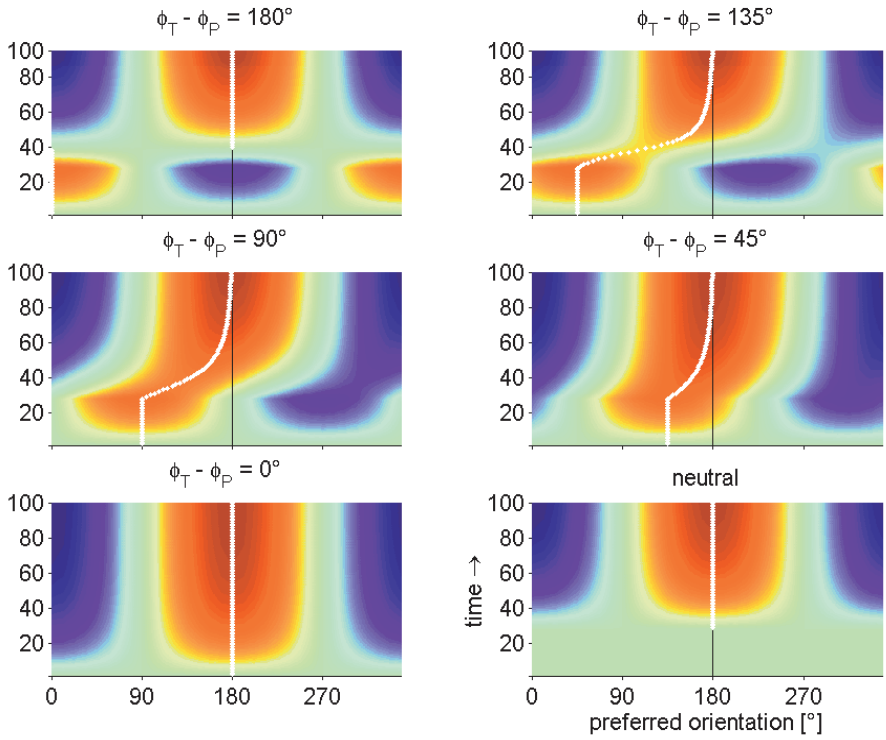


Figure 65: Time course of activity of accumulators and the direction of their resulting population vector (white marks). Activation strength is color-coded ranging from .27 (blue) to .73 (red), baseline is .5 (green). SOA was 28 cycles and target direction was 180°. The first 28 circles show the buildup of prime-related activation in accumulators. After onset of the target, the activity distribution shifted towards accumulators that had the same preferred direction as target orientation. The population vector did not overshoot, i.e. it was always on the side on which the prime was presented.

3.5 Discussion

Introducing directionally tuned accumulators enabled the population-vector model to represent multiple stimulus orientations and response alternatives. Predicted reaction time functions of the model were ordered by the degree of congruence, which is in line with the largest part of experimentally observed priming effects. What is not explained by the model is the experimental finding that primes with the highest degree of incongruence (180°) did not produce the longest reaction times, while the other reaction time functions were ordered by congruence (figures 23 and 62). Moreover, the population-vector model and the original accumulator model by Vorberg et al. both predict higher slopes of the priming function $RT_{180°} - RT_{0°}$ than was observed experimentally (figures 14 and 63). Gaze trajectories in the experiments, reported in chapter two, showed deviations in their trajectories, which cannot by accounted for by the model. If, for example, a target pointing to the left (180°) was preceded by a prime pointing upwards (90°), gaze deviations in experiment 1 had a downward component. If the prime had a leftward component, the deviation had a rightward component. Especially in saccades with late onset, deviations were directed away from prime-orientation. The model, however predicts, that the population vector, which represents response tendencies, shifts from prime-related activity to target related activity without overshooting. In its present version, the population-vector model cannot explain, how deviations contralateral to prime direction can arise.

3.6 The effect of response suppression

A mechanism, which might be able to account for the observed movement deviations, is suppression of prime-related activity. Assume that the target points to the left, but the prime has prepared an upward movement. If accumulators represented both response tendencies with equal strength, a compromise would result; the movement would be directed to the upper left (figure 66, panel A). In order to correctly reach the target location, prime-related activation has to be inhibited. But with primes and targets having overlapping activity, inhibition of prime-related activity has the side effect that also some accumulators are inhibited, which are needed for the representation of the target (figure 66, panel B). The result is that inhibition of prime-related activation biases responses: If the prime had an upward component, the movement triggered by the target would have an additional downward component. The next section contains simulations of the population-vector model, which incorporate suppression.

A B

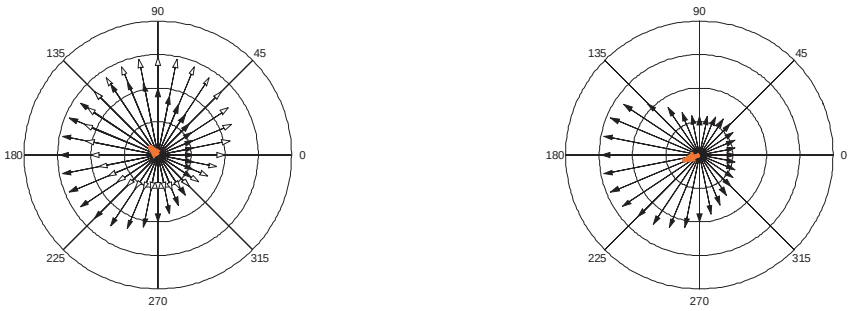


Figure 66: **A**, Polar plot of prime-related (open arrows) and target related (filled arrows) activation of accumulators. Arrow direction indicates each accumulator's preferred direction. State of activation is depicted by arrow length. **B**, Inhibiting accumulators that participate in the representation of the prime would affect the representation of the target, too. As a result the population vector driven by the target would lack some of its upper left components. This would result in a population response biased to the lower right, compared to presentation of the target alone.

3.6.1 A mechanism for response suppression

Accumulators are broadly tuned, each responding to stimuli with a variety of orientations. When an accumulator is driven by separate stimuli which require different responses, a conflict occurs. It has been suggested that neurons might solve this conflict by changing their receptive field properties, for example by shrinking their rezeptive-field size or by suppressing irrelevant information (Moran and Desimone, 1985). With cosine tuning curves as described above, primes pointing far away from target direction do not create much response conflict in neurons which represent the target, and therefore they do not require inhibition. But the closer prime and target direction are, the more suppression of the distracting prime is required (see figure 67). This strategy, however, creates a paradoxical situation. When primes and targets are congruent, suppression is strongest. A solution to this problem is suggested by Schall and Hanes (1993) following investigation of neurons in the frontal eye fields of monkeys. Schall and Hanes presented stimuli at different peripheral locations, to which eye movements were required. When stimuli were presented alone (detection), neurons showed broad tuning functions peaking at their preferred direction. However, if stimuli were presented simultaneously with seven distractors of equal eccentricity from fixation as the target (search task), the shape of the tuning function changed. The peak was still highest at the preferred direction, but if a stimulus was presented near the preferred direction of a neuron (60-120° off center), responses were suppressed. If stimuli were presented farther away from the preferred direction, responses were unchanged compared to the detection task.

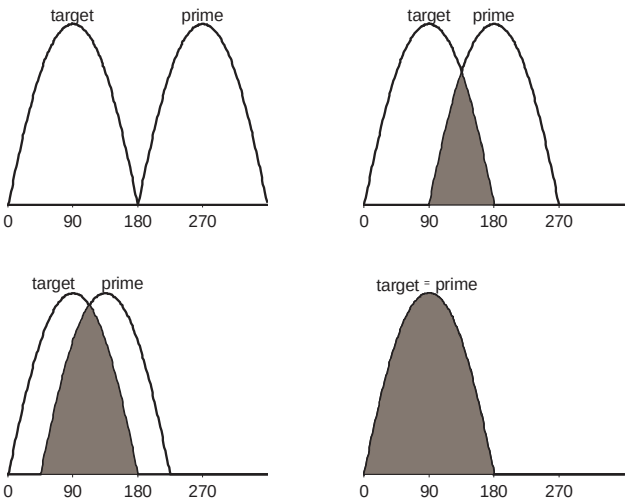


Figure 67: Primes and targets drive distinct populations of neurons when they point to opposite directions. When prime orientation gets closer to target orientation the number of mutually driven units increases leading to a stronger response conflict which increases suppression of prime-related activation.

3.6.2 Simulating priming with response suppression

In the following simulation, the onset of a target created a decaying inhibitory input so that accumulators were suppressed, which represented directions nearby to target direction. Accumulators representing directions far away from target orientation or target orientation itself, were spared from suppression. Such a function was incorporated to the model by multiplying the activity distribution at target onset with a spatial filter centered around target orientation (figure 68). The spatial filter was the difference of two gaussian functions. One determined the width of inhibition around target orientation, and the other determined the range around target orientation which was to be spared from inhibition. For each accumulator an inhibitory input was determined for the time of target onset by

$$\text{suppression}(\Delta_\phi, |\mathbf{a}(t)|) = (e^{\frac{-\Delta_\phi^2}{2\sigma^2_{excitatory}}} - e^{\frac{-\Delta_\phi^2}{2\sigma^2_{inhibitoy}}})|\mathbf{a}(t)| \quad (5)$$

with Δ_ϕ being the angular difference between target orientation and the accumulator's preferred direction in radians, and $|\mathbf{a}(t)|$ the accumulator's activation at target onset. Suppression decayed at a rate .975 with each further processing cycle.

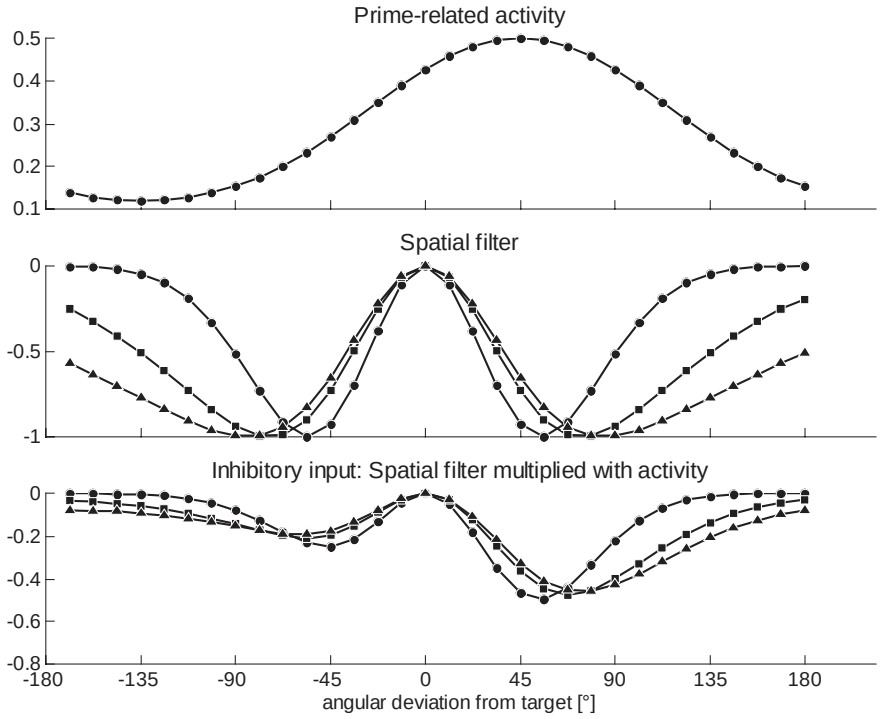


Figure 68: Construction of a multiplicative inhibitory gradient around target direction. **Top panel**: Activity caused by a prime with 45° direction. **Center**: Spatial filter defined by the sum of an inhibitory ($\sigma_{inhibitory}$ = 0.75, 1.5, 2.25) and an excitatory ($\sigma_{excitatory}$=.625) gaussian, both centered around the target (direction 0°). **Bottom:** Inhibitory input is the product of prime-related activity and the spatial filter. Note that suppression is asymmetric due to higher prime-related activity at 45° than at –45° (reference point 0° is target direction).

3.6.3 Predicted reaction times

With suppression of primes, the predicted reaction time functions were still ordered by congruence, but effects were smaller than in the model without suppression (figure 69).

A **with suppression** **B** **without suppression**

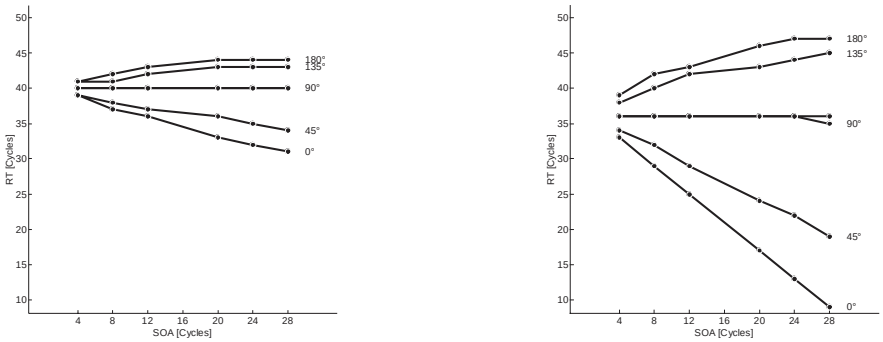


Figure 69: Response times as a function of congruence and SOA predicted by **A**, the model with, and **B**, without suppression.

The priming effect was fitted by the function $RT_{180°} - RT_{0°} = .455$ SOA + 1 cycle. With prime suppression the model can account for priming effects having slopes below 1.

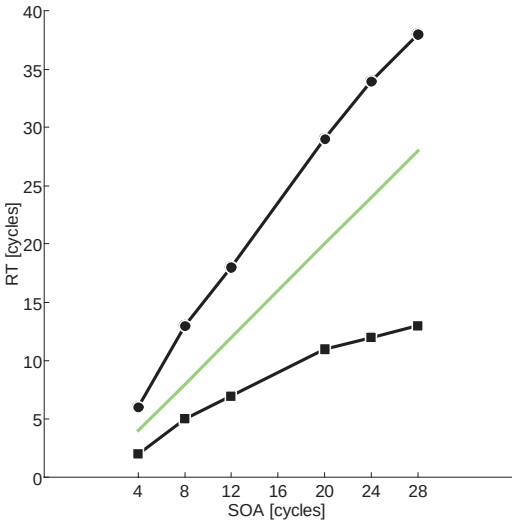


Figure 70: Priming effect for the model without (circles) and with suppression (squares). Predicted reaction times for maximally congruent (0°) trials were subtracted from maximally incongruent trials (180°). The priming effects increase linearly with SOA but with different slopes (1.33 without and .455 with suppression). The diagonal shows a theoretical priming effect with unit slope where the priming effect equals SOA.

3.6.4 Movement deviations

The onset of the target created a decaying inhibitory input to the accumulators that was centered on the target. The shape of the distribution of inhibition depended on the distribution of prime-related activation in the accumulators at target onset (figure 71). The figure illustrates that the shape of inhibitory input depended of congruence between prime and target. Inhibition was either symmetric or asymmetric. Symmetry of inhibition depended on whether prime-related activation was symmetrically aligned with target orientation, which is only true for phase shifts which are a multiple of π. Symmetric inhibition was predicted for 180°, 0° and neutral congruence. Asymmetric inhibition was predicted for all other congruence levels.

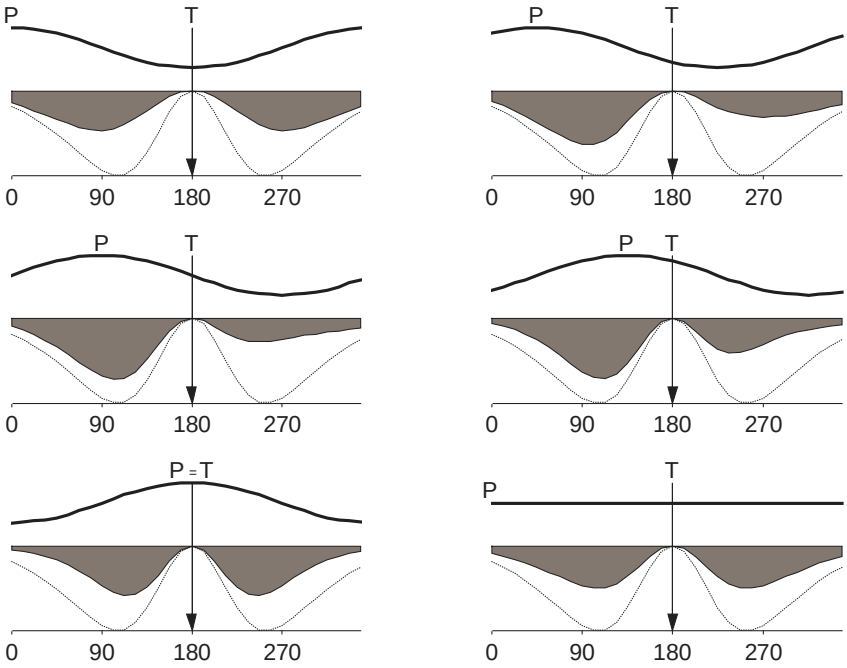


Figure 71: Inhibitory input (gray) for prime suppression is the product of the spatial filter aligned with the target and prime-related activation at target onset (P). The dotted line represents the spatial filter that is centered on the target (T). Target orientation was fixed at 180° under all congruence levels, which are shown in different panels. **Upper left**: 180°, **right**: 135°, **center left**: 90°, **right**: 45°, **lower left**: 0° (congruent), **right**: neutral.

Suppression of prime-related activation by a gradient centered on target direction produced deviations of the population vector qualitatively different from the simulations without suppression. With asymmetric suppression (45, 90, and 135° conditions), the population vector had an orientation pointing away from prime orientation. In the simulated example the primes of the 45, 90, and 135° congruence conditions were all pointing in the upper half field. After presentation of the target, the population vector moved towards target direction, but overshot, so that it had a small downward component. The simulations support the assumption that prime suppression has caused the deviations of gaze trajectories reported in the experimental part.

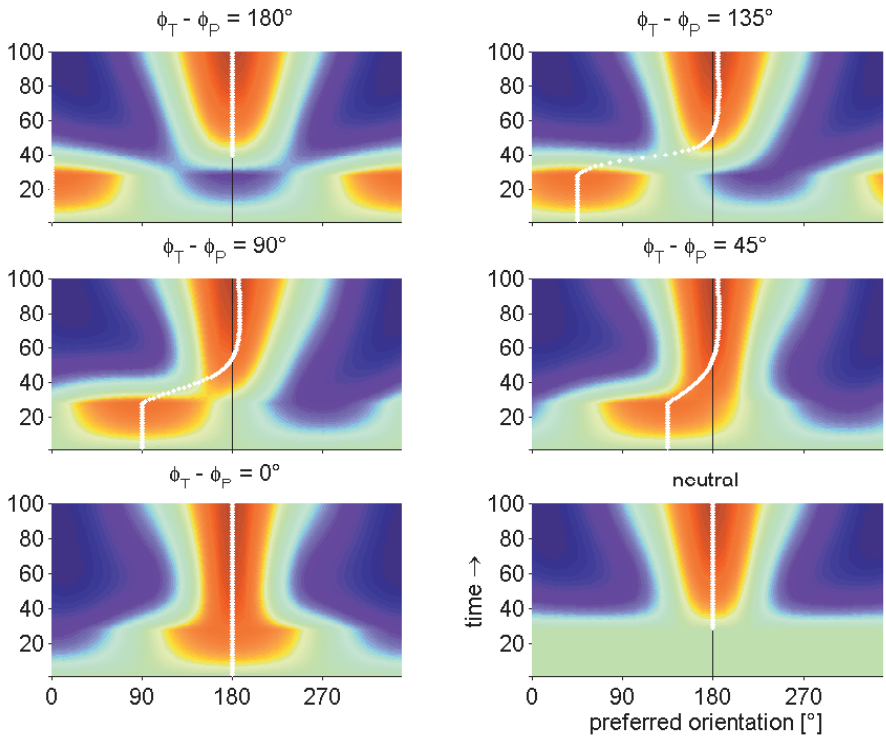


Figure 72: Time course of activity of accumulators and the direction of their population vector (white marks). Activation strength is color-coded ranging from .27 (blue) to .73 (red), baseline is .5 (green). SOA was 28 cycles and target direction was 180°. The first 28 circles show the buildup of prime-related activation in accumulators. After onset of the target, the activity distribution shifts towards accumulators that have the same preferred direction as target orientation. In contrast to the previous simulation (figure 65), suppression lead to an overshoot of the population vector away from prime orientation. This is illustrated by the crossing of the horizontal median (black vertical line).

Moreover, as in the experiments, the size of gaze deviations was SOA-dependent (figure 73). Suppression strength depended on the strength of prime-related activation. With longer SOA, there was more time for the primes to drive accumulators, which had to be inhibited after onset of the target. Consequently, for longer SOAs the model predicts stronger deviations away from the prime. These deviations are not predicted for situations with symmetric inhibition. This prediction is in line with the experimental data. Directional gaze deviations were observed with 45, 90, and 135° congruence, only.

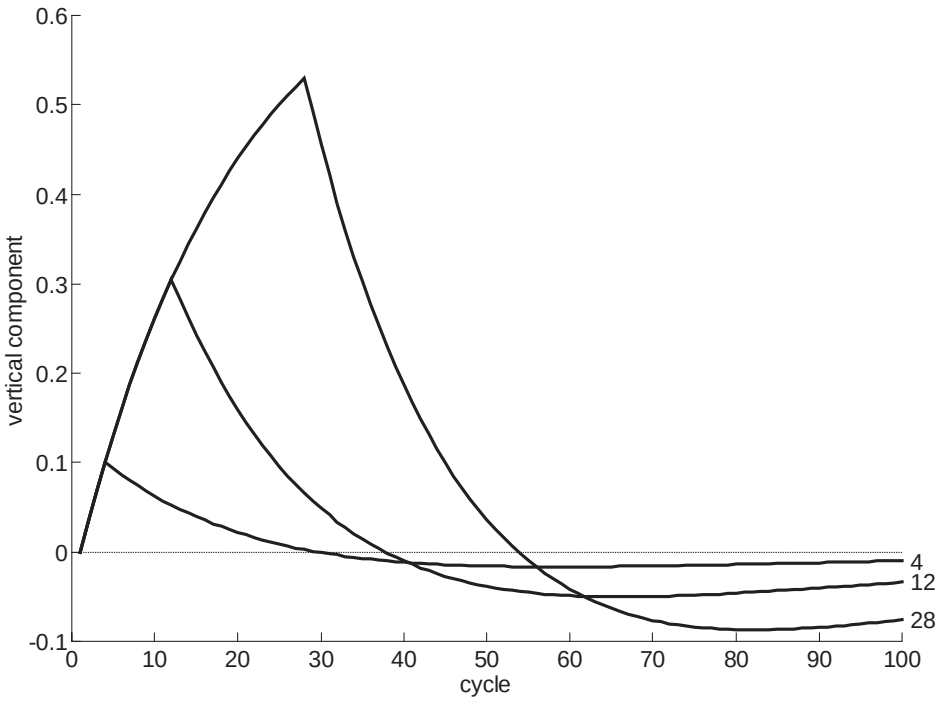


Figure 73: Vertical component of the population vector for an upwards-oriented prime and a leftwards-oriented target (congruence = 90°) for different SOAs (4, 12, 28 cycles). The dotted line indicates the horizontal median. The population develops towards the prime, with longer SOA leading to stronger prime-related activation. Suppression starts at target onset. Suppression strength depends on the strength of prime-related activation. Consequently do longer SOAs lead to stronger deviations away from the prime.

3.7 General Discussion

The pattern of congruence effects in priming of eye movements was captured by a model which assumed that processing of directional information in eye movements is population-coded and represented by neural units which, over time, accumulate evidence for the presence of their preferred stimuli. The model was a population-vector extension of an accumulator model presented by Vorberg et al. (in prep.). Priming effects were ordered by congruence in the experiments as well as in the simulation. The experimental observations of priming effects with slopes smaller than unit slope was a challenge for the accumulator model of Vorberg et al. as well as for the population-vector model presented here, as the observed slopes were out of the range of possible slopes predicted by both models.

Deviations of gaze trajectories as well as slope of the priming function led to the assumption that prime-related activity might have been suppressed. Suppression of conflicting information was observed by Moran and Desimone (1985) in stimulus selection processes of neurons in the inferior temporal cortex. Neurophysiological data of movement-related neurons in monkey frontal eye field (Schall and Hanes, 1993) indicated that this mechanism might operate in response selection of eye movements as well. Suppression occurred only when conflicting information of different locations, which were candidates for a goal directed eye movement, fell into the receptive fields of the same movement-related neuron. Establishing suppression in the model, produced overshooting deviations of the population vector, contralateral to the direction indicated by the prime. The simulations replicated the overshooting gaze deviations in the reported experiments. Without suppression, the model predicted that motor deviations were always bound between directions indicated by prime and target, respectively. With suppression the model predicted that there was always an overshoot contralateral to prime orientation.

The experimental data showed, that both kinds of deviations occurred in the same experiment and within the same subject. Analyzing gaze deviations in conjunction with response speed revealed that saccades with early onsets produced deviations towards prime orientation whereas saccades with late onsets deviated away from it. Taking a look back at the activation of accumulators in figures 72 and 73 shows that such a pattern was inherent in the time course of the population vector. During the early phase after target onset, the population was biased towards the prime. Deviations away from prime orientation were prominent in later phases only. If onset of movement was free to occur at different points in time, the population would exhibit a bias towards prime orientation with early onset, and contralateral to prime orientation with late movement onset.

The model assumes that the population vector simultaneously reflects decision and response preparation processes. This implies that the time course of activity in accumulators determines movement onset and direction. Whether this is a viable assumption can only be investigated in a model which also allows reaction time variability. Different implementations of reaction time variability might produce different predictions for movement deviations. If reaction time variability was an effect of varying threshold from trial to trial, the predictions were straightforward: Low thresholds lead to an early movement onset with a response tendency biased towards prime orientation. With higher threshold and longer reaction time, suppression effects lead to an overshoot of the population vector and response tendency is biased away from the prime. Although the predicted movement deviations are in line with the experimental observations in chapter two, there is neurophysiological evidence that reaction time variability is not caused by varying threshold but by varying processing rate (Hanes and Schall, 1996). How variable processing rates of accumulators would influence the behavior of the model is a complex issue, because it is unknown how rate variations of different neurons are correlated and whether the same laws apply for inhibitory and excitatory processes.

It is not intended to claim by the architecture of the model, that decision processes and motor preparation processes are located within the same neural substrate. It is reasonable to assume that the contrary is true, and that the model just depicts converging operations from motor related substrates as the superior colliculus, working memory aspects mediated by the dorsolateral prefrontal cortex and suppressive actions of the frontal eye fields. Grouping together all these processes in a single population of accumulators is certainly wrong at some point or the other, but on the other hand the success of capturing the effects of congruence and stimulus asynchrony in priming may indicate that decision processes and movement preparation are implemented in the brain with similar processing mechanisms, namely, accumulation, and that they rely on population coding as their common principle of neural representation.

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